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CHEMICAL CONTROL OF POLYDORA WEBSTERI AND OTHER ANNELIDS INHABITING OYSTER SHELLS

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ABSTRACT

A number of chemical compounds were tested and found either to compel Polydora websteri and nereid worms to emerge from oyster shells or to kill them directly within the shells. Compounds which caused more than 50 per cent of both groups to emerge from shells within three hours were considered effective vermifuges. Compounds which killed more than 50 per cent of worms within the same time were considered effective vermicides. The most efficient vermifuges for P. websteri were benzene and ethylene compounds. Common salt was the most practical vermicide tested because it is simple to use, inexpensive and kills worms quickly.

Worms of the genus Polydora, commonly called mud-blister worms, are serious pests. They not only form unsightly black areas on the inner faces of oyster shells, rendering infested oysters undesirable for half-shell trade, but also make oyster shells brittle. There are several published reports of attempts to use chemicals to control these worms. Among them is that of Korringa (1951) who reports that P. hoplura and P. ciliata can be killed by immersing infested oysters for three hours in sea water containing di-nitro-ortho-cresol at 500 parts per million or by placing oysters for 16 hours in fresh water; and Mackin and Cauthron (1952) observed that a solution of phenol at 500 ppm in sea water causes P. websteri to emerge. These authors do not state the rate at which worms leave the shells.

During the screening of a large number of chemical compounds for possible use in combatting shellfish enemies, a study carried on at Milford since 1946, several compounds have been found which are more effective against P. websteri, the species which occurs in southern New England waters, than those proposed by earlier workers. Two categories of compounds could be used in control of these worms: (1) vermifuges, chemicals that cause worms to emerge from their tubes and leave the oyster shell, and (2) vermicides, chemicals that kill worms within their tubes, but do not ordinarily cause emergence.

Oysters heavily infested with P. websteri were gathered from uncultivated beds in West Tisbury Great Pond on Martha's Vineyard Island. They were kept in wire baskets in Milford Harbor until 24 hours prior to their use when they were brought into the laboratory and allowed to become acclimated gradually to room temperature. For each

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experiment two oysters, each in a separate finger bowl, were submerged in a nine-liter container of the solution to be tested.

In initial tests each compound was tried at a concentration of 100 ppm. Following each test, oysters were kept in warm running sea water for five to eight days to allow any living worms to recover from the effects of the compound tested. They were then placed for 24 hours in a solution of O-dichlorobenzene at 100 ppm which was found to cause almost 100 per cent emergence of both Polydora and nereid worms. Thus, a group of eight oysters which yielded an average of 88.7 P. websteri and 10.7 nereids per oyster upon initial treatment gave only one or two worms per oyster on the second treatment with this chemical. Any worms which survived the initial test could be collected and counted by this method. Because oysters immersed for 24 hours in a 100 ppm solution of O-dichlorobenzene may die, this treatment was used merely to insure 100 per cent emergence of worms. As many as 332 P. websteri were recorded for a single oyster.

The effectiveness of vermifuges was calculated directly by comparing the number of worms emerging in the experimental vermifuge with the number emerging in the subsequent treatment with O-dichlorobenzene. Since no simple method exists for quantitatively removing from oyster shells worms that have been killed in situ, it was necessary in evaluating vermicides to use the average number from the eight oysters mentioned above as the total worm population and the number emerging on subsequent treatment with O-dichlorobenzene as survivors of various chemicals. Obviously, the data for effectiveness of vermicides are less accurate than those for vermifuges.

Over 30 compounds caused some P. websteri to emerge, but only those causing 50 per cent of worms to emerge within three hours are considered effective vermifuges (Fig. 1). Of these, O-dichlorobenzene was selected as the most practical vermifuge because at concentrations below 100 ppm it is more effective than monochlorobenzene, trichloroethylene and tetrachloroethylene. Moreover, the latter two compounds are quite volatile and may be somewhat dangerous to people handling them on a large scale. One compound more effective than O-dichlorobenzene, 4-nitrobenzene-azo-resorcinol, is difficult to dissolve in sea water and is expensive. Phenol is not an effective vermifuge at concentrations much below 500 ppm, e.g. at 100 ppm it caused emergence of only about 33 per cent of the worms. Naphthalene might be effective, but is difficult to dissolve in sea water. When added to O-dichlorobenzene, however, enough of it goes into solution to increase the effectiveness of the O-dichlorobenzene. Certain nereid vermifuges, such as emulsifiable rotenone, Bulan crystalline, and Tris (acetoxy methyl) nitro methane, caused P. websteri to retract into their tubes but did not cause emergence.

Usually it required about five or six minutes for the first P. websteri to emerge, probably because it takes about that long for the chemical to penetrate the worm's tube. Worms usually back away from

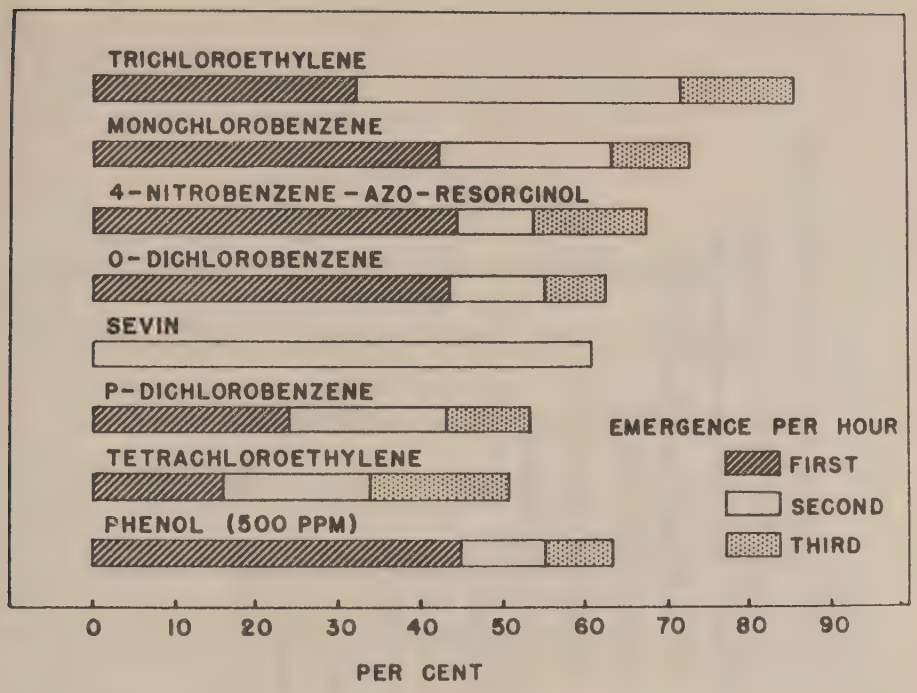

Fig. 1. Rate of emergence of P. websteri from oyster shells during exposure to 100 ppm solutions of various chemicals for three hours. Only those compounds that were more than 50 per cent effective are shown. Rate of emergence was not determined for Sevin.

chemicals and emerge posterior end first. Since they do not swim, worms drop to the bottom of the pans and, if removed to another vessel containing untreated sea water and some bottom detritus, they soon begin building new mud tubes.

Nereid worms appear to be more sensitive to certain chemicals than P. websteri and react to them more quickly (Fig. 2). Since they do not live in long narrow tubes and contact a chemical with their whole bodies, nereids usually begin to emerge as soon as oysters are placed in the solution.

Several compounds killed P. websteri within their tubes (Fig. 3). Di-nitro-ortho-cresol at 100 ppm killed few worms. At 500 ppm, however, the concentration which Korringa (1951) used, 81.4 and 90.5 per cent were killed by exposures of one and three hours, respectively. A 500 ppm solution of 2-chloro-1-nitro propane killed 96.6 per cent of the worms within three hours. Victoria Blue at 200 ppm killed 82 per cent with only a 5-minute immersal; 89 per cent were killed within 10 minutes; and 97 per cent, within 15 minutes. Actually, the lethal effects of this dye on annelid worms were discovered at this laboratory before the

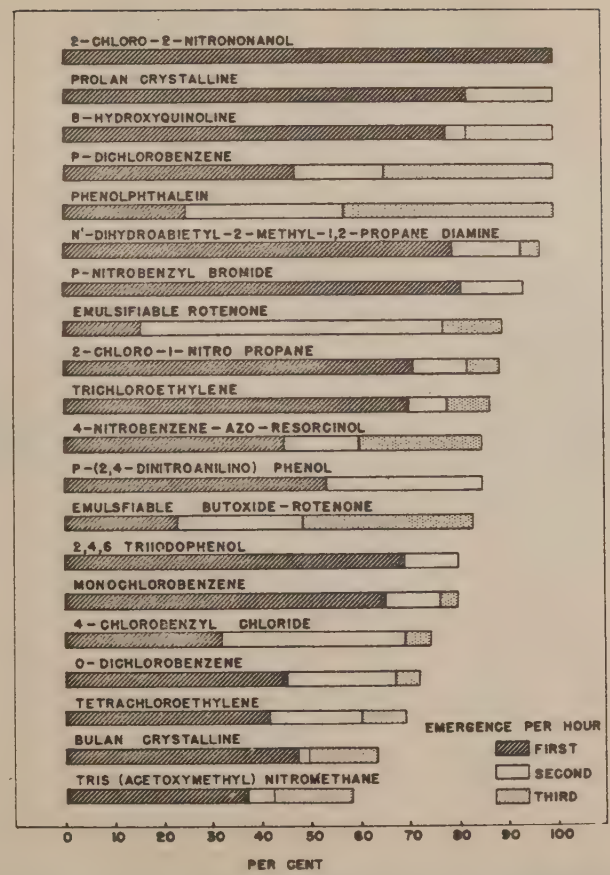

Fig. 2. Rate of emergence of nereids from oyster shells during exposure to various chemicals at 100 ppm for three hours.

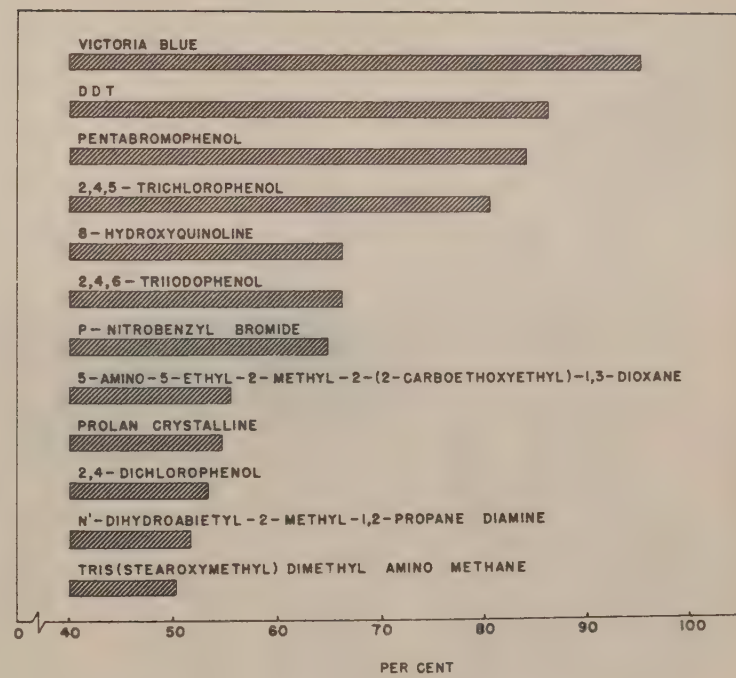

Fig. 3. Mortality of P. websteri in oyster shells after exposure to various chemicals at 100 ppm for three hours.

present study, and this compound has been used routinely during the last four years to exterminate worms in clam hatchery troughs. The above compounds, except 2-chloro-1-nitro propane, were also lethal to nereids as were other compounds listed in Figure 4.

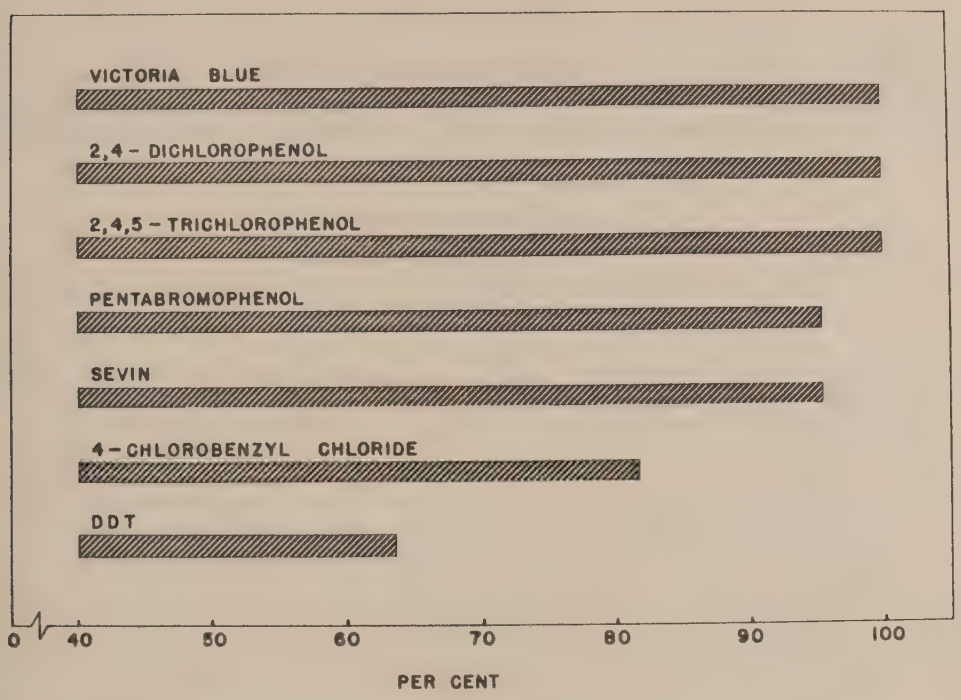

Fig. 4. Mortality of nereid worms in oyster shells after exposure to various chemicals at 100 ppm for three hours.

Perhaps the most practical compound for worm control is common salt. From 87 to 98 per cent of P. websteri were killed by a 10- to 15-minute dip in a saturated salt solution followed by 15 or more minutes of drying in air. Shorter dips required a longer period of drying to kill worms, but even a 1-minute dip was 89 per cent effective when combined with a drying period of at least two hours. These studies showed that it is almost impossible to kill every P. websteri in an oyster shell within three hours.

At low concentrations several compounds apparently acted as inhibitors to P. websteri. For example, in 2-chloro-1-nitro propane the worms neither extended their tentacles as in feeding nor emerged. When combined with vermifuge 4-nitrobenzene-azo-resorcinol, worms emerged only as the concentration of the inhibitor was decreased (Table 1).

Table 1. Comparison of numbers of P. websteri emerging within three hours from shells of two oysters in a 10 ppm solution of vermifuge 4-nitrobenzene-azo-resorcinol in the presence of an inhibitor, 2-chloro-1-nitro propane, at various concentrations.

Concentration of inhibitor in ppm	Number of worms emerging	Number remaining alive in shells
50	37	103
20	63	48
10	77	78
5	112	67
0	158	35

Inasmuch as oysters stay closed while immersed in solutions of most chemicals, they are usually not harmed by them. They pump intermittently, however, in benzene and ethylene compounds; hence, these compounds may be lethal if the immersal is too long. In O-dichlorobenzene at 100 ppm, for instance, an immersal of three hours caused little mortality of oysters, but one of 24 hours killed almost all of them. At the end of this period oysters gaped widely and did not recover after being placed in running sea water. They also pump in a solution of Victoria Blue, which, even if the concentration is low, accumulates in their tissues and eventually kills them. Consequently, in these experiments we used Victoria Blue in fresh water which kept oysters closed and therefore prevented them from absorbing the dye. Oysters with chipped bills (7 of 40) could not keep the dye out and eventually died.

We believe these vermicides can be applied in commercial oyster culture. Oystermen could use them to kill worms in shells of oysters in spring, thus giving oysters a chance to deposit layers of white shell over the black mud blisters by fall. This treatment, however, would not prevent setting of young P. websteri which could form small blisters at the periphery of shells. A saturated solution of salt appears to be most practical for oystermen, because it is simple to use, inexpensive, requires only a short exposure to kill worms, and kills some other fouling organisms as well (Loosanoff 1957). The other compounds would be difficult to maintain at precise concentrations. Vermifuges could be used in various ways in studies of the biology of worms and of oysters. To cause all worms to emerge without harming oysters, infested oysters could be alternately immersed in O-dichloro-

benzene for not longer than three hours in which the worms will emerge and then in sea water for recovery of the oysters, until all worms have emerged.

ACKNOWLEDGMENTS

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SHORTER COMMUNICATIONS

Collection and descriptions of juvenile tunas from the central Pacific*

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(*Received* 21 *February*, 1961)

Abstract—Collections of juvenile tunas during the period 1951–60 from the central Pacific are recorded. Juveniles of *Neothunnus macropterus* (TEMMINCK and SCHLEGEL), *Katsuwonus pelamis* (LINNAEUS), and *Auxis* sp. are described and figured. Initial results with the British Columbia midwater trawl, as modified for collecting tuna forage organisms and juvenile tunas, suggest that this trawl has considerable promise as a collecting device. Its ability to catch juvenile tuna appears much greater than that of the 10 ft Isaacs-Kidd midwater trawl.

ALTHOUGH much has been learned in recent years about the biology of adult tunas, we still have very little information concerning the occurrence, distribution, and habits of their postlarval and juvenile stages. This lack is due mainly to poor success in collecting the young with the methods hitherto used, i.e., dipnetting at night-light stations, midwater trawling with small and medium-sized nets, seining with tuna bait nets, and searching the stomach contents of adult tunas and other pelagic fishes. Most of the juveniles recorded in the litertature have been reported from scattered localities and have come either from the stomachs of pelagic fishes (KISHINOUYE, 1919, 1923, 1924, 1926; INANAMI, 1942; MARR, 1948; ECKLES, 1949; SHIMADA, 1951a; YABE, ANRAKU and MORI, 1953; YABE *et al.*, 1958) or from dipnetting at nightlight stations (SCHAEFER and MARR, 1948a, 1948b; WADE, 1949, 1950; SHIMADA, 1951b; KLAWE and SHIMADA, 1959). Since tuna juveniles are taken sporadically, generally in small numbers, it is important that all known captures be recorde d so that the information will be available to investigators.

As a part of their research on the biology of the tunas, staff members of the Honolulu Biological Laboratory (HBL), United States Bureau of Commercial Fisheries, have been trying since 1951 to collect young tunas with only moderate success (TABLE 1). Recently, during the period 20 October to 8 November 1958, a series of test hauls was made with a British Columbia midwater trawl (BARRACLOUGH and JOHNSON, 1956), modified with a cod-end of ¼ in. mesh. The results (TABLE 2)

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indicate that this trawl will be an effective instrument for collecting juvenile tunas.

Two types of hauls, horizontal and 3-step oblique, were made. In the first the trawl was lowered to the desired depth, where it was towed horizontally for 1 hr. In the second the trawl was lowered to the desired depth (usually 300–350 ft) and then towed horizontally for 20 minutes at each of three levels : 300, 200 and 100 ft. The results (Table 2) provided several valuable bits of information. First, it was evident that the 3-step oblique pattern gave a higher percentage of hauls in which juvenile tunas were taken (57%) than did the horizontal pattern (25%). Second, a statistical comparison using the Mann-Whitney *U* test (SIEGEL, 1956) did not indicate any significant difference (one-tailed $p = 0{\cdot}473$) in juvenile tuna captures between hauls made at night (2000 hr. local time) and in the day (0800 hr. local time). Third, the British Columbia trawl took juveniles up to 52·5 mm long in mid-ocean, whereas earlier captures of fish this size were all near land. Juvenile tuna were taken by the trawl at distances from the nearest land of 280 to 540 miles, the latter being the greatest distance from land at which the gear was used.

Since no day–night difference was found in the catches, data for all 3-step oblique hauls were combined for comparing performance of the British Columbia trawl with that of a 10 ft. Isaacs-Kidd trawl which had been used by HBL for collecting young tuna (Table 3). The upper section of TABLE 3 shows that the sampling conditions for the two trawls were comparable, except for the depth of the haul. This difference is corrected, however, by expressing the catch in terms of juveniles per unit of water strained between the surface and the 300 ft. depth. A comparison made on this basis shows that the British Columbia trawl caught 43·6 per cent more juveniles than the 10 ft. Isaacs-Kidd trawl. If we assume that juvenile tunas were equally abundant in the area where both cruises were made, and there are no strong reasons for believing otherwise, then the higher catch made with the British Columbia trawl must be due to the greater efficiency of the trawl for this purpose. This higher efficiency was probably due to the larger mouth opening (111·7 m^2 in the British Columbia trawl as against 8·2 m^2 in the 10 ft. Isaacs-Kidd trawl) and, to some extent, to the speed of hauling (average of 3 knots as against 5 knots). Since juveniles of the sizes taken in trawls (up to 52·5 mm) are probably already fairly rapid swimmers, they would be expected to be able to dodge a small net more easily than a large one. If the smaller net were hauled at high speed to overcome this dodging, it would very likely increase net noise and luminescence to such an extent that the fish would become aware of the net early enough to avoid it. Consequently, it is conceivable that a net with a large mouth opening, hauled at a slower speed, may be much more effective in capturing juvenile tunas. The higher catches obtained with the British Columbia trawl appear to support this hypothesis.

Of the juvenile tunas in the HBL collection, species identifications have been made for *Neothunnus macropterus* (TEMMINCK and SCHLEGEL) and *Katsuwonus pelamis* (LINNAEUS). A num berof juveniles recognized as *Auxis* could not be assigned to species (see later discussion). Three unidentified specimens, although recognized as scombrid, could not be identified either to genus or species because they were badly damaged.

Juvenile *N. macropterus* (FIG. 1) are characterized by a relatively deep body; a short snout, equal to or less than the diameter of the eye; a completely black first dorsal fin, the edge of which forms a convex outline; and the absence of pigmentation on the thoracic and abdominal areas. Other pigmentation on the body includes heavy concentrations or bands along the mid-lateral line and along the dorsal edge. Dorsal to the mid-lateral line are faint patches of pigment which develop into five or six vertical bars on larger juveniles.

As in adult *N. macropterus*, a 22·6 mm juvenile cleared and stained in alizarin red *S* has 39 vertebrae (18 precaudals and 21 caudals), and the first haemal spine is similar to the spines following it. The gillrakers on the first arch are not fully developed in this specimen (2 + 16), but the 46 mm specimen in FIG. 1 already has enough gillrakers (7 + 21) for positive identification. The 21 gillrakers on the lower limb of the arch is identical with the number found in the adult (usually 20–21).

Four other species of thunnids have been recorded from the central Pacific where our juveniles were obtained. Since the possibility exists that our juveniles may be any one of these, it is important that any similarities or differences be examined. *Parathunnus sibi* (TEMMINCK and SCHLEGEL), which generally has 18 or 19 gillrakers on the lower limb of the first gill arch, was eliminated, since our 46 mm juvenile already has 21 gillrakers. Two other speices, *Thunnus orientalis* (TEMMINCK and SCHLEGEL) and *T. thynnus* (LINNAEUS), which may be synonymous, were eliminated because they generally have 22–23 gillrakers on the lower limb. The albacore, *T. germo* (LACÉPÈDE), is the only species having a gillraker count for the lower limb (generally 20, often 21) similar to that of our juvenile, but it was eliminated on the basis of the shape of the first haemal spine (YABE *et al.*, 1958).

Table 1. Record of juvenile tuna collection in the central Pacific by the Honolulu Biological Laboratory by gear and methods other than the British Columbia midwater trawl

Date	*Latitude*	*Longitude*	*Katsuwonus pelamis*	*Neothunnus macropterus*	*Auxis sp.*	*Unidentified*	*Total*	*Fork length* (mm)	*Method of capture*
25 April 1951	2° 11·0′ N	153° 08·0′ E (South of Caroline Is.)	5	0	0	0	5	39–44	Dipnet[1]
3 May 1951	6° 20·5′ N	162° 22·0′ W (Kingman Reef, Line Is.)	34	0	0	0	34	20–34	Dipnet
25 May 1951	2° 51·0′ N	157° 03·0′ W (South of Caroline Is.)	6	0	0	0	6	23–55	Dipnet[1]
30 May 1951	5° 18·0′ N	159° 49·0′ E (South of Caroline Is.)	12	0	0	0	12	21–49	Dipnet[1]
20 June 1951	2° 01·5′ N	171° 37·0′ W (Near Phoenix Is.)	4	2	0	0	6	16–19	Dipnet
21 June 1952	5° 56·0′ N	139° 26·0′ W (Mid-ocean)	1	0	0	0	18	18	6 ft. beam trawl[2]
9 April 1953	20° 35·0′ N	157° 32·0′ W (Hawaiian Is.)	1	0	0	0	1	18	1-M ring trawl[2]
3 June 1954	1° 44·0′ N	158° 15·0′ W (North of Jarvis Is.)	0	0	0	1	1	<20	6 ft. Isaacs-Kidd trawl[2]
1 February 1955	29° 56·0′ N	179° 28·0′ E (Northwest of Kure Is.)	0	0	0	2	2	20; 60	10 ft. Isaacs-Kidd trawl[2]
5 February 1956	6° 20·5′ N	162° 22·0′ W (Kingman Reef, Line Is.)	5	0	0	0	5	45–58	Dipnet
26 September 1956	0° 02·0′ N	159° 50·0′ W (North of Jarvis Is.)	1	0	0	0	1	22	10 ft. Isaacs-Kidd trawl[2]
27 January 1958	8° 49·0′ S	140° 04·5′ W (Near Marquesas Is.)	7	0	0	0	7	23·5–34	Stomach of *N. macropterus*
28 February 1958	7° 42·0′ S	140° 10·0′ W (Near Marquesas Is.)	3	0	3	0	6	31–52	Stomach of *N. macropterus*
22 May 1959	20° 47·0′ N	157° 28·0′ W (Hawaiian Is.)	1	0	0	0	1	49	Bait seine[3]
13 August 1959	(Vicinity of Oahu, Hawaiian Islands. Position not available)		6	1	7	0	14	30–73	Regurgitated by *K. pelamis*[3]
Totals			86	3	10	3	102		

[1]Ego and Otsu, 1952.
[2]King and Iversen (unpublished manuscript).
[3]Commercial live-bait fishing vessel, M.V. *Bonito*.

Table 2. Results of trawling for juvenile tunas with a modified British Columbia midwater trawl on cruise 47 of the Hugh M. Smith[1]

Sta. No	*Date*	*Latitude*	*Longitude*	*Type of haul*	*Maximum depth of tow* (ft.)	*Zone time*[2]	*Katsuwonus pelamis*	*Neothunnus macropterus*	*Auxis sp.*	*Total*	*Fork length* (mm)
19	20 October	15° 20′ N	153° 40′ W	Horizontal	450	2107	0	0	0	0	—
32	27 October	0° 02′ S	149° 32′ W	Horizontal	310	1315	0	0	0	0	—
33	27 October	0° 01′ N	149° 44′ W	Horizontal	300	2010	0	0	0	0	—
37	30 October	4° 58′ S	150° 00′ W	Horizontal	300	0845	12	0	0	12	14·5–26
38	30 October	4° 58′ S	149° 52′ W	Horizontal	740	1312	0	0	0	0	—
39	30 October	4° 57′ S	149° 56′ W	Horizontal	320	2013	0	0	0	0	—
41	31 October	5° 00′ S	150° 00′ W	Horizontal	40	0807	0	0	0	0	—
44	31 October	5° 01′ S	150° 00′ W	Horizontal	30	2025	0	0	0	0	—
46	1 November	5° 00′ S	149° 58′ W	3-step oblique	340	0845	7	0	0	7	10–30
47	1 November	3° 38′ S	149° 56′ W	3-step oblique	350	2012	0	0	0	0	—
49	2 November	2° 09′ S	149° 47′ W	3-step oblique	320	0843	3	0	0	3	23–29
51	2 November	0° 44′ S	149° 46′ W	3-step oblique	320	2013	4	0	4	8	18·5–52·5
53	3 November	0° 37′ S	149° 58′ W	3-step oblique	310	0838	3	0	0	3	19·9–21·7
56	4 November	1° 56′ N	150° 09′ W	3-step oblique	310	1030	0	0	0	0	—
58	4 November	2° 56′ N	150° 03′ W	3-step oblique	340	2013	1	0	0	1	13·9
60	5 November	4° 28′ N	150° 29′ W	3-step oblique	350	0820	0	0	0	0	—
62	5 November	6° 06′ N	150° 28′ W	3-step oblique	340	2017	1	2	0	3	14·6–22·6
64	6 November	7° 39′ N	150° 16′ W	3-step oblique	320	0823	1	0	0	1	24·1
66	6 November	9° 08′ N	150° 03′ W	3-step oblique	350	2005	0	0	0	0	—
68	7 November	10° 40′ N	149° 52′ W	3-step oblique	340	0825	0	0	0	0	—
70	7 November	12° 13′ N	149° 56′ W	3-step oblique	350	2015	1	0	0	1	6·8
72	8 November	13° 53′ N	150° 01′ W	3-step oblique	450	0817	0	0	0	0	—
	Totals						33	2	4	39	

[1]Research vessel of the U.S. Bureau of Commercial Fisheries.

[2]Starting time for each tow.

Fig. 1. A 46 mm *Neothunnus macropterus* regurgitated by adult *Katsuwonus pelamis*, off the island of Oahu, Hawaiian Islands.

Fig. 2. A 47 mm *Katsuwonus pelamis* captured in dipnet at Kingman Reef, Line Islands.

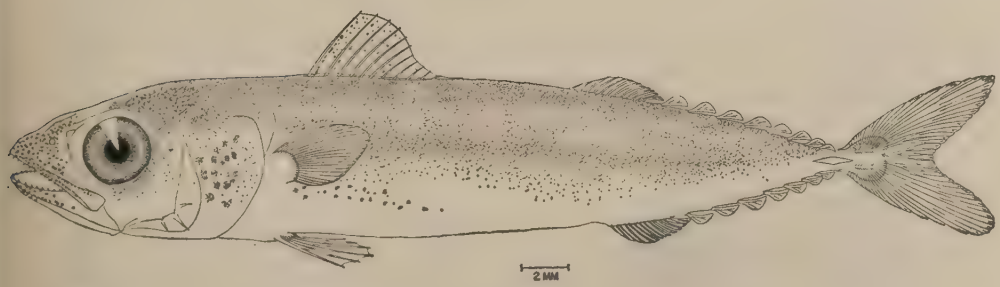

Fig. 3. A 39 mm *Auxis* sp. captured in a modified British Columbia midwater trawl at 0° 44′ S, 149° 46′ W.

YABE's study indicates that *T. germo* as small as 124 mm (standard length) can be identified by this spine, which appears laterally compressed. I examined one of YABE's specimens measuring 184 mm and noted that the width of the flat first haemal spine was nearly twice that of the second. The second spine and those following it were normal, as in other tunas. In our specimens the first haemal spine was not compressed but was similar to the second spine. Thus, on the basis of the number of gill-rakers on the lower limb of the first gill arch and the shape of the first haemal spine, it seems reasonable to assume that our juveniles are *N. macropterus*.

Table 3. Comparison of the performance of the British Columbia and 10–foot Isaacs-Kidd midwater trawls in collecting juvenile tunas

	British Columbia trawl	*10 ft. Isaacs-Kidd trawl*[1]
Trawling data :		
Vessel[2] and cruise number	*Hugh M. Smith* 47	*Hugh M. Smith* 35
Area : latitude	14°N – 5 °S	10 °N – 5 °S
longitude	150 °W	143 °W – 160 °W
Dates	20 Oct. – 8 Nov. 1958	15 Aug. – 1 Oct. 1956
Depth of haul	0 – 350 ft.	0–600 ft.
Type of haul	1-hour 3-step oblique	1-hour oblique
Number of hauls	14	13
Total volume of water strained (500,000 m^3)	18·73	0·99[3]
Results :		
Total juveniles captured	27	1
Juveniles per 500,000 m^3 of water strained	1·44	1·01

[1]Data for the Isaacs-Kidd trawl from KING and IVERSEN (Unpublished manuscript).
[2]Research vessel of Honolulu Biological Laboratory, U.S. Bureau of Commercial Fisheries.
[3]Calculated on the basis of a sampling depth of 0–300 ft for comparison with the British Columbia trawl.

Juvenile *K. pelamis* (FIG. 2) are easily identified by the characteristic pigmentation of the first dorsal fin and its concave outline, the moderately long snout, and the number of vertebrae. The first dorsal fin has scattered chromatophores on the first 3 or 4 interspinal membranes and along the distal edge of the remaining membranes. The only other genus in which the juveniles are known to have the first dorsal fin shaped like that of *K. pelamis* is *Euthynnus* (SCHAEFER and MARR, 1948a; WADE, 1950; MEAD, 1951; MATSUMOTO, 1959). In *Euthynnus*, however, the first dorsal fin is either completely or almost completely pigmented, as in *N. macropterus*. Furthermore, unlike *Euthynnus* and *N. macropterus*, juveniles of *K. pelamis* do not develop vertical bands of pigmentation on the dorsal half of the body during the early stages of growth. The snout, measured from its tip to the anterior edge of the eye, is much greater than the diameter of the eye.

Examination of 4 cleared and stained juveniles (19, 27, 33, and 52 mm) revealed 41 vertebrae (20 precaudals and 21 caudals), which is definitive for *K. pelamis*.

The young of *Auxis* (FIG. 3) are easily recognized by the narrow body, the widely separated first and second dorsal fins, and the very light pigmentation of the first dorsal fin. In addition, all specimens have a black spot at the isthmus, a characteristic seen only in one other genus, *Euthynnus* (MEAD, 1951; MATSUMOTO, 1958, 1959). In juvenile *Euthynnus* however, the first and second dorsal fins are continuous.

It is known that two species of *Auxis*, the short-corseleted *A. thazard* (LACÉPÈDE) and the long-corseleted *A. thynnoides* (BLEEKER), occur in the Pacific (KISHINOUYE, 1923; FOWLER, 1938; WADE, 1949; MATSUMOTO, 1960). Although the adults of this species are separable by corselet morphology, this character is useless for separating juveniles below 200 mm in length, because the corselet scales are not fully developed. Consequently no definite species identification of our *Auxis* specimens has been made.

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EXTRAIT

Rapp. et Proc.-Verb Vol. 150, 1961
Cons. Internat. Explor. de la Mer

SECTION I
SYSTEMATICS AND NATURAL MARKS

Discussion Leaders: Dr. GILES W. MEAD and Dr. CARL J. SINDERMANN

Section A

Alverson, D. L., & Westrheim, S. J. "A review of the taxonomy and biology of the Pacific Ocean perch and its fishery".

Kelly, G. F., Barker, A. M., & Clarke, G. M. "Racial comparisons of redfish from the western North Atlantic and the Barents Sea".

Kotthaus, A. "Contributions to the race problem in redfish".

Kotthaus, A. "Preliminary remarks about redfish otoliths".

Phillips, J. B. "Problems in the identification of fishes, with a comparison between shallow-water and deep-water species of *Sebastodes* (Scorpaenidae)".

Templeman, W., & Pitt, T. K. "Vertebral numbers of redfish, *Sebastes marinus* L. in the north-west Atlantic, 1947–1954".

Travin, V. I. "A brief survey of Soviet investigations in redfish (*Sebastes* genus)".

Trout, G. C. "*Sebastes viviparus* (Krøyer) and the redfish problem".

Section B

O'Rourke, F. J. "An immunological and chromatographic study of *Sebastes marinus* L. and *Sebastes mentella* Travin".

Schaefer, H. "A biochemical contribution to the redfish problem".

Sindermann, C. J. "Parasitological tags for redfish of the western North Atlantic".

Sindermann, C. J. "Serological studies of redfish".

Templeman, W., & Squires, H. J. "Incidence and distribution of infestation by *Sphyrion lumpi* (Krøyer) on the redfish, *Sebastes marinus* L. of the western North Atlantic, 1949–1953".

Since the section devoted to a discussion of "natural marks" (serological, parasitological, and biochemical) and that devoted to the methods and results of systematics studies, are directed toward a common end, a joint report of the results of these two sections is submitted here.

The participants in this symposium have recognized the two parallel taxonomic aspects of the redfish problem. The first is the systematic nature of the population of North Atlantic *Sebastes* in an evolutionary sense and is concerned with ancestry, biological or reproductive isolation and gene flow, and speciation and variation in a rather comprehensive sense. The second aspect is a more pressing one of direct concern in fishery assessment and management: what population units, or stocks, can be delimited for management purposes, and whether such definition can be attempted in the immediate future. These two aspects are comparable, and the full answer to the problem in a systematics sense would provide complete answers to the questions asked by students of population dynamics and the fishery.

The several contributions to the symposium on morphological variation and the separation of populations by anatomical differences, although to some extent inconclusive, have helped to define the problem and to clarify our understanding of it. Dr. Krefft has provided a provocative hypothesis concerning the origin of the North Atlantic *Sebastes,* particularly the American forms known as *mentella*-type and the eastern Atlantic *marinus*-type, from two subspecies of the related and more primitive genus *Helicolenus (H. dactylopterus maderensis* and *H. d. dactylopterus* respectively) or their predecessors.

Similarly, in a discussion not presented to the symposium in written form, Mr. B. B. Parrish has provided notes on the criteria necessary to the assessment biologist in any consideration of "stocks". Similar remarks were presented in Mr. Gulland's contribution to this symposium. Since Mr. Parrish's comments will not

appear elsewhere, we have included a part of them in this report, as follows:–

"Whereas the taxonomic status of 'groups' of fish is of major importance in the proper understanding of the evolution and genetics of the group, population studies are interested, principally, in identifying unit stocks or management units which can be treated as separate dynamic groups. Thus 'groups' of very different taxonomic status can, as dynamic groups, have the same significance in population management".

"The essential property of a unit stock, as a management unit, is that it is sufficiently self-contained biologically so that its abundance (number and weight) is determined by factors operating within its boundaries, which affect either recruitment, growth or mortality. A consequence of this is that any fishery management procedure will operate principally on the parameters of that defined group."

"The specific demands in the unit stock concept will, in fact, vary according to the type of management measure under consideration. For some types, e. g. control of age of first capture, the principal requirements are 'groups' of 'uniform' growth-rate and mortality, but for some others, the demand is for more 'complete' biological groups".

"In many instances there is wide biological variation within the boundaries of a single taxonomic group, and often there are major differences between the sexes in growth, maturation, etc. In population studies these differences may be of greater importance than differences between taxonomic groups. Further, it may sometimes be possible to treat two or more distinct taxonomic groups, having similar population parameters, together for assessment purposes".

"Essentially, the major task with *Sebastes* at present is to look for geographical boundaries between groups within its total distribution, for which, despite much variation, there is some evidence of uniformity about its population parameters." (End of quotations from Mr. Parrish.)

It has become apparent during this symposium that satisfactory answers can be provided for but few questions. It has become equally apparent that answers or at least close approximations must be had now. The conclusions which follow may represent the concensus of the participants in the systematics and natural marks discussions.

1. *Sebastes viviparus* is a species clearly distinct from its congeners in general form, structure of otolith, fin ray, vertebra and scale complement, colour, growth-rate, and perhaps other features. It is common in waters more shallow than those of the larger species but does occur throughout the depth range of the commercial populations. *S. viviparus* has been found from East Greenland and Iceland eastward to Great Britain, the Faroes, and the coast of Norway. There are indications that *S. viviparus* is more closely allied to the American *mentella*-type redfish than to the eastern Atlantic forms. Since it is easily recognizable and not important in the commercial landings, it need be of no further interest in population dynamics problems.

2. The commercial American fishery for redfish in the north-west Atlantic is based upon the *mentella*-type redfish which may constitute three stocks for assessment purposes. The first of these lives in waters comprising ICNAF Subareas 4 and 5, and Division 3 O and 3 P (the south-west Grand Banks and westward to the Gulf of Maine and including the Gulf of St. Lawrence). The second area is ICNAF Division 3 K, 3 L, and Subarea 2 (the northern Grand Banks, the Newfoundland shelf, and the coast of Labrador). These two groups intermingle in Division 3 N, the south-eastern Grand Banks, in which the situation is not yet clear. The third area is Division 3 M (Flemish Cap).

The restriction of reproduction in the north, and the restrictive influence which the Gulf Stream waters will have on the eastward drift of viable larvae in the south, together with suspected larval drift patterns in the area, contribute to the isolation of these populations. There may be local variation within these populations, for the studies of parasite infection reported by Dr. Templeman and Dr. Sindermann, and the analysis of vertebral counts reported by Dr. Templeman, show that these fishes are chiefly non-migratory. Further suggestions of slight geographical variations were demonstrated in Mr. Kelly's morphometric analysis. The growth-rates reported by Mr. Kelly and Mr. Sandeman were similar, the sexes being considered separately. The occasional *marinus*-type individuals, and the local inshore populations of peculiar behaviour such as the Eastport, Maine, population discussed by Mr. Kelly, should be excluded for assessment purposes.

3. From the morphometric data available, the known growth-rates, behavioural patterns, the structure of the otolith, and lastly the biochemical distinctions discussed by Professor O'Rourke, it seems apparent that Barents Sea *mentella*-type and *marinus*-type *Sebastes* must be considered distinct for population analyses, whatever the systematic status and relationship of each may be.

4. In the absences of discrete characters for the separation of *marinus*-type from *mentella*-type redfish in the East Greenland/Iceland/Faroes area, we concur with the conclusion reached by Dr. Kotthaus: that the separation of types in this area is at the present time difficult and in many instances impossible. The possible influence of length of pelagic life in this area, food preferences, conditions at time of spawning etc., on morphometry was discussed, and the concensus was that much more information of the first few years of life would be required before a meaningful taxonomic

analysis would be possible. The opinion that the intermediate types abundantly represented in Dr. Kotthaus's material could be allocated to one type or another was expressed. In the absence of objective criteria for a more complete separation, no conclusion could be reached. Biochemical and serological methods could appropriately be applied to a study of these intermediates. A similar approach could be used to establish the distinctiveness, or the relationships, of the "giant" fish occasionally found in most areas.

5. Biochemical and serological characteristics offer definite promise of providing information of value to the study of redfish groups.

6. Opinion was divided on the usefulness of otolith form as an indicator of environmental conditions, races, subspecies or species. It is obvious that in certain areas otolith type is a species or type characteristic, but it is equally obvious that a great deal of geographical variation exists.

Several suggestions for future work seem in order:—

(a) Available data on the American *mentella*-type commercial redfish stocks, as tentatively defined above, should be reviewed by biologists in the ICNAF area with respect to the parameters essential to assessment and management, prior to the further application of an assessment programme.

(b) In view of the potential value of biochemical and serological methods for studying systematics and populations of fish, these methods should be encouraged in the analyses of redfish populations of the North Atlantic. There are several ways in which they could be assisted by ICES and ICNAF.

(i) By encouraging senior university staff biochemists and serologists with grants in aid and summer employment at fisheries laboratories;

(ii) by arranging for the preparation and publication of a handbook describing various methods used;

(iii) by encouraging government employment of serologists and biochemists in fisheries laboratories;

(iv) by arranging a world meeting, possibly in conjunction with the forthcoming FAO conference on fish physiology, of those working with serological and biochemical approaches to fish taxonomy.

(v) It is further recommended that certain biochemical determinations be accomplished at sea on freshly-caught individuals.

(c) Whereas the eastern, and the western, *mentella*-type and *marinus*-type redfish can be distinguished visually in the Barents Sea and the more northern American waters, less progress has been made toward the separation of types in more central areas. A study of the changing characteristics of these types, starting with the more northern areas, should be attempted in an effort to interpret the nature of the intermediate types prominent in data such as that presented by Dr. Kotthaus.

(d) One recommendation proposed by Dr. H. Einarsson and included in his report on the "larval studies" discussion is of particular significance to the taxonomic question. The further study of larval characteristics, particularly the pre-extrusion larvae in the ICES area and the planktonic larvae in the waters south and west of Greenland, is essential.

(e) The morphological data presented by Dr. Kotthaus and Mr. Kelly do not separate adequately the redfish types found between East Greenland, Iceland, and the Faroes. Similarly, an adequate explanation of larval peculiarities such as the differing length-frequency modes reported by Mr. Vagn Hansen and Mr. K. P. Andersen may involve taxonomic as well as reproductive factors. Reproduction, pelagic life and its duration, food preferences and growth, etc., have a direct bearing on taxonomy; the accumulation of information bearing on these questions is vitally needed.

(f) Attempts to provide objective criteria, including colour and other field characters, for the separation of *mentella*- and *marinus*-type redfish should continue.

(g) The possible effect of environment on body form, the behaviour of larvae, and many other questions of importance in taxonomy and redfish biology in general was reflected in all discussions. Many of these questions could be resolved if redfish and their young could be kept in controlled aquaria. The occurrence of redfish in shallow water, such as the Eastport, Maine, population studied by Mr. Kelly, provides a source of material for such experimental work, and it is strongly urged that such studies be undertaken whenever and wherever the opportunity may arise.

of this study can only be accomplished through a tagging program. Use of internal tags has been successfully applied to pelagic fish such as herring. Efficient recovery of tagged fish has been a major problem. A research and development program designed to perfect a better tag detecting system resulted in the design of a radioactive magnetic tag, tag injection equipment, and associated detection and ejection machinery. The equipment has been designed to detect radioactive tags at high speeds and under heavy radiation masking conditions with 100 percent efficiency. The system costs a fraction of that required to fabricate less efficient magnetic and metallic detectors. Appropriate safety features are an integral part of the system, which has been granted an AEC license. The technique is currently undergoing field evaluation in southeastern Alaska.

SURVIVAL OF PINK SALMON AT LITTLE PORT WALTER RESEARCH STATION

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Little Port Walter is a research station operated by the Bureau of Commercial Fisheries to study pink salmon biology. In most recent years, pink salmon have comprised the major part of Alaska's commercial fishery harvest, and it is vitally important that factors controlling their abundance be known. Despite many years of study in Alaska, British Columbia, and Washington, the interaction of these controlling factors is only beginning to be understood.

Two of these factors which seem to be important in the early freshwater life history of pink salmon at Little Port Walter are: time of spawning, and stream gradient and its association with survival.

Little Port Walter is located on Sashin Creek at the southern end of Baranof Island, southeastern Alaska, about 60 miles south of Sitka. This location was selected for studying pink salmon mainly because it is on the very edge of the commercial fishery, minimizing the complicating effects of a fishery on marine survival.

Adult pink salmon have been counted at a weir at Little Port Walter annually since 1934, and seaward migrating fry have been counted each spring since 1940. These counts provide the longest continuous record of pink salmon production on the Pacific Coast. Other data that have been recorded and analyzed include air and water temperatures in the stream and in the gravel, rainfall and stream discharge, and length-weight, sex, and fecundity of adult salmon.

Freshwater Survival

Little Port Walter environmental conditions do not fluctuate widely and do not seem to be a major cause of fluctuations in survival. We have been unable to demonstrate any consistent relationship between survival of eggs and fry and air or water temperature, or even rainfall, although some mortality is evident during extreme floods. There is also little evidence that predators in the stream are an important factor.

The only factor that has consistently affected survival is time of spawning. This relationship of spawning time to survival of fry was first report by Skud in a paper that appeared in Copeia in 1958. His conclusions were based on data through 1955; since then, five more years of data have conclusively shown that survival is invariably greater when spawning is early. Furthermore, since 1950, the odd-year runs have always been earlier than the even-year runs. Thus, highest survival occurs every other year. Between 1950 and 1959, the dates on which 50 percent of the run passed the weir were, on the average, 12 days earlier for odd-year runs than for even-year runs (September 1 and 13). The most probable reason for higher survival from earlier runs is that water temperatures are dropping during this season, and eggs get a head start in development before cold winter weather retards development. Laboratory experiments have shown that the most vital and sensitive period of development is immediately after fertilization. In the even years, when eggs are deposited later in the season, they do not reach an advanced stage of development before the onset of cold weather and are thus more sensitive to environmental conditions.

In the fall of 1959, an unprecedented large run of pink salmon totaling 35,000 returned to Little Port Walter, the largest run since 1942. Several factors combined to produce this large run: the 1957 parent run spawned earlier than any other run in the station's history, which coincided with a

high survival of fry (22.4 percent); a large absolute number of seaward migrating fry (585,000); and a high marine survival (6.1 percent). This large spawning run provided an opportunity for comparison of spawning characteristics with small runs of previous years.

The major obvious difference between the large and small runs was the distribution of spawning fish. In most recent years, when runs have been small, spawning has been concentrated in the lower part of Sashin Creek. This lower stream is characterized by moderate gradient, fine gravel (averaging walnut size), and uniform depth. The general appearance of this lower section is what biologists would judge to be ideal for salmon production. The upper stream, in contrast, has a steep gradient, coarse gravel with many large rocks and boulders, and water depths ranging from periodically exposed bars to deep pools.

This difference in distribution of spawners was in itself not remarkable and might be expected because of population pressures. An additional significant fact came to light in the spring of 1960 incidental to another project. To estimate total fry production from the stream, a series of 303 square-yard areas, distributed randomly throughout the stream, were excavated by pumping a water-air mixture into the gravel. It was noted that the greatest density of live fry was in the upper steep section where there had been fewer spawners. Thus, this area was far more productive than the lower-gradient section near the mouth of the stream.

The actual causes of this survival differential are unknown, but it is certain that gradient, if not a factor *per se*, is at least associated with survival at Little Port Walter.

Discussion

The biological implications of early versus late spawning and of high gradient versus low gradient production with large and small runs are most significant:

Pink salmon invariably mature at two years of age, so alternate years' runs comprise separate races even in the same stream. For unknown reasons, it is characteristic of pink salmon runs to be alternately large and small in adjacent years. At Sashin Creek in recent years the odd-year runs have been larger than even-year runs, and odd-year runs have

spawned earlier and have had higher survival than even-year runs. This has made the odd-year runs inherently more productive than even-year runs, and has tended to preserve alternating years of large and small runs.

Furthermore, small runs choose the less productive low-gradient stream area for spawning, and portions of large runs utilize the more productive high-gradient stream areas. This tends to maintain the numerical differential between alternate large and small runs, augmenting the large runs and depressing the small ones.

It would be premature at this time to extrapolate the data from Little Port Walter to other streams, as it is not known whether the same phenomena occur in other areas. A great deal of further study over a wide geographical range is needed to determine whether they are generally applicable.

A METHOD OF SEPARATING RIVER STOCKS OF RED SALMON IN THE BRISTOL BAY FISHERY

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The fishery for red salmon (Oncorhynchus nerka) in Bristol Bay is confined by regulation to the immediate vicinity of the mouths of the Bay's five major river systems. This restriction results in five fishing districts, each of which is separated from others by 30 to 40 miles of coastal waters which are closed to fishing.

Red salmon stocks destined for the different spawning systems intermingle while passing through the several fishing areas.

A method of separating the commercial catch of each district into its component stocks is presented in this report. In the simplest case the method is based upon the assumption that the proportional frequencies of a particular character (age group frequency distributions used as an example) in the commercial catch is dependent only upon the rates of intermingling of several stocks within the fishing areas.

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REMARKS CONCERNING THE BENEFITS OF SYSTEMATIC AND REPETITIVE COLLECTING FROM NAVIGATION BOUYS.

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(Abstract)

When buoys are brought in for periodic cleaning and servicing by the Coast Guard, many attached or clinging species of marine life are available for study. By observing, by sampling, and by recording the data a wealth of scientific information is uncovered. Research along this line offers unusual opportunities for study, some of which are discussed below.

A study of the fouling organisms found on buoys at different latitudes along the coastline will reveal not only the dominant species in a given area, but also the geographical limits of many species at the surface. If the buoy chain and mooring are available, vertical distribution of species can be studied at the same time.

Many thousands of a single species often settle on a buoy and with this material variation within a species can be defined. Or perhaps, using the same material, an investigator might prefer to work out the great changes in gross morphology that occur in the early postlarval to juvenile stages. Another approach could be a study of the settling habits and mechanics of attachment of the early postlarval forms, or of the orientation and adaptation of species.

Because buoys are out for known lengths of time, it is possible to define the limits of the spawning season as well as to determine rates of growth for some species after having systematically collected from many buoys in an area. Mortality studies can be attempted with these same data. Surface temperatures are available at many offshore places along the coast so that the relationship between species and temperature can also be established.

The spawning grounds, the length of the larval period, the direction and rate of speed of water currents—these and other indirect issues can be given at least theoretical consideration as more and more information becomes available through such studies.

Each buoy has its own complex community—a totality of related parts. Scientific contributions resulting from planned marine research using this harvest cannot help but further the progress towards a better understanding of some of the biological intricacies involved.

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SOME OBSERVATIONS ON THE GROWTH AND SURVIVAL OF ORGANISMS ON THE SHELL OF *PLACOPECTEN MAGELLANICUS*.

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(Abstract)

The post-larval commensal species which grow and flourish on the upper valve of the sea scallop, *Placopecten magellanicus*, include representatives of most marine phyla. Most commonly noticed are the boring sponges, sea anemones, branching and encrusting bryozoans, pelecypods, barnacles, tube worms, and simple and colonial ascidians. The species found on the shells are those which are found on any suitable substrate in the vicinity.

A single species may settle in large numbers on a scallop, but more often a mixed group of organisms settle. As the community on the host grows and thrives, other organisms may join it, usually simply to browse thereon or to take shelter in available crevices. Thus, the attached life may form a veritable "garden" on many sea scallops. The fact that the "garden" is simply a fouling community is often apparent when a fast growing dominant is found to have overgrown, crowded, or smothered less fortunate members.

Some commensals may divide or bud asexually (sponges and actiniarians) but usually the increase in bulk and weight is through increase in size and weight of the individuals which first settled. Young sea scallops are quite active and usually collect little growth on their shells, but adults become more or less sedentary and may be heavily fouled. The heavily fouled individuals carry their burden without apparent harm. They are, of course, not hindered in the same respect as crawling gastropods which search actively for their food. Perhaps the greatest burden a sea scallop might be forced to bear is the sponge, *Cliona celata*, which, besides boring into the host's

shell, often forms large, irregular masses 8 to 10 inches high over the surface of the shell.

(Kodachrome slides accompanied this paper.)

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SHELL MORPHOLOGY IN THE LARVAL AND POSTLARVAL STAGES OF THE SEA SCALLOP, *Placopecten magellanicus* (Gmelin)

BY ARTHUR S. MERRILL

WITH THREE PLATES

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SHELL MORPHOLOGY IN THE LARVAL AND POSTLARVAL STAGES OF THE SEA SCALLOP, *Placopecten magellanicus* (Gmelin)

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WITH THREE PLATES

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By Arthur S. Merrill[1]

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INTRODUCTION AND ACKNOWLEDGMENTS

The larval and postlarval stages of many species of pelecypods have been studied and reported by various investigators over the years. Stafford (1912) and Sullivan (1948), working with species from the northeast coast of North America, have contributed materially to our knowledge of several species. However, the sea scallop, *Placopecten magellanicus* (Gmelin), has received very little attention. Sullivan's study did not include the species, and Stafford only devoted half a page to it. Consequently, efforts to identify the early stages of the sea scallop by means of the existing literature have met with little success.

Attempts at rearing larvae of the sea scallop have also been unsuccessful (Drew, 1906; Posgay, 1953; Baird, 1953). Therefore, it has been necessary to compare the changes and modifications through an extensive series of specimens in order to identify the early stages of the species with certainty.

There is evidence that past investigators have experienced difficulty in identifying the young of the sea scallop. Dall (1898, p. 726) lists an excellent synonymy which includes several specific names thought to be new species but which later were found to be young sea scallops.

The primary purpose of this paper is to describe and figure

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development of shell characters through the early stages of this commercially important species with the hope that it will allow future workers to quickly and accurately identify it at any stage of growth. Descriptions of the adult stage are included when it is necessary to describe later development of a particular character.

Little has been written of the early life history of the sea scallop. Jackson (1890) described and figured specimens he thought to be young *P. magellanicus* but which proved to be *Cyclopecten nanus,* a species subsequently described and figured by Verrill in 1897 (see Merrill, 1959). Drew (1906) fully described and figured both the shell and the animal of the adult, but his attempts to rear the young were unsuccessful and he was only able to discuss and figure the very early stages of embryogeny covering the first 5 days after fertilization. Stafford (1912) was able to identify *Pecten* larvae found in the plankton collected in his area but I am not convinced he could identify them with certainty below generic rank. His last paragraph about scallops on page 239 is ambiguous. If I interpret correctly, he ends his discussion by concluding that the *P. magellanicus* in his figure 35 is *Pecten islandicus.* In any case, he based his identity of allied species of *Pecten* on the differences in size of the settling larvae, but others (Jörgensen, 1946; Sullivan, 1948; Loosanoff and Davis, 1950) have found larval size to be quite variable within a species. My own observations agree with this. Morse (1919, p. 152, fig. C) does little more than figure, without measurements, the general outlines of an early stage of the sea scallop. The figure, as he says, resembles certain avicular forms. Borden (1928) gives measurements of pecten larvae, all under 0.2 mm., taken from plankton tows. However, her description of the larval form at about 0.3 mm. is incorrect, which suggests that the still younger larval forms under 0.2 mm. may not have been correctly identified. Baird (1953) published an interesting paper on the finding of a large number of tiny sea scallops on Bryozoa. However, his work is not descriptive; rather, he discusses the unsuccessful laboratory attempts to rear sea scallops beyond the trochophore stage and relates his findings to age and growth in small scallops. The present author (Merrill, 1959) described and compared the juvenile sea scallop with a somewhat similar appearing species, *Cyclopecten nanus* Verrill, but found it beyond the scope of that paper to describe and figure the various early stages of shell morphology in the sea scallop.

The material used in this study came from several sources. Sea scallops were reared in this laboratory at Woods Hole, Massachusetts, through the straight-hinge stage. A large sample of minute sea scallops was collected from a navigation buoy brought in to the Coast Guard Station at Woods Hole, Massachusetts, in June 1958. Nearly 10,000 of these tiny shells were measured, of which 80 per cent were under 4 mm., the smallest 0.5 mm., the largest 13.2 mm. Several samples were taken from other buoys as well as from the ocean bottom during the year 1958. In these samples, sea scallops as small as 0.25 mm. were collected. This is about the size at spatfall when the scallops are undergoing metamorphosis. Samples of large sea scallops taken from various stations along the coast were also available for study. The author also had ample opportunity to observe and compare the structures and variations not only in these but in other small scallops accumulated over the years from several sources by personnel of the Bureau of Commercial Fisheries, Biological Laboratory, at Woods Hole, Massachusetts.

The methods used in cleaning the minute completed larval shells, and in separating and mounting the valves are those described by Rees (1950, p. 75).

The term *height* refers to the distance from the umbo to the ventral margin; *length* to the distance from the anterior to the posterior edge (see Fig 1).

Acknowledgments are due the following individuals without whose help and cooperation the value of this work would have been considerably lessened. To Mr. Julius A. Posgay and Doctors Robert L. Edwards and Roland L. Wigley of the Bureau of Commercial Fisheries, Biological Laboratory, at Woods Hole, Massachusetts, and to Doctors William J. Clench and Ruth D. Turner and Mr. Robert Robertson of the Mollusk Department in the Museum of Comparative Zoology at Harvard University, I am greatly indebted for advice and comments after reading the manuscript. To Mr. Robert Brigham, staff photographer of the Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, and Mr. Frank White, staff photographer in the Biological Laboratories at Harvard University, I owe much for the quality of the photographs reproduced herein. I am also grateful to Mr. Frank Bailey of the Bureau of Commercial Fisheries, Biological Laboratory, at Woods Hole for the excellent line drawings.

THE LARVAL SHELL

A prodissoconch or first-formed larval shell, strikingly different from the succeeding dissoconch, is easily seen in young post-larval specimens of *P. magellanicus* (Pl. 2, fig. 1). The prodissoconch is distinctly separated from the dissoconch by a sharp line. This heavy concentric line denotes the end of the free-swimming pelagic period of the tiny scallop.

The larval development is usually divided into two stages. The first is the "straight-hinge stage" in which the veliger produces the embryonic "D-shaped" shell. This is followed by the "umbo stage" in which the shape, texture, and hinge structure are sufficiently differentiated to allow identification.

The straight-hinge larva of the sea scallop is similar to that of other lamellibranchs. It has a wide hinge-line, is relatively long in proportion to its height, and is almost equally rounded at both ends (Pl. 1). The two valves are hinged dorsally, the margins meeting ventrally and laterally. The minuteness of the shell, its transparency, and lack of structure leave few characters of importance to aid in identification at this early stage. Both valves are similar in size, shape, and curvature. They are fairly flat, and lack color. The hinge-line is usually straight, but in occasional specimens, it curves inward slightly. The size ranges from 60 to 80 microns in height and 80 to 115 microns in length in 7-day-old laboratory-reared specimens.

At the umbo stage, as seen in the completed prodissoconch, the valves are discoidal, inflated, and nearly equal in size, shape and curvature, the upper valve being slightly more convex. The structure of both valves is homogeneous, opaque, non-prismatic, and with exceedingly fine lines of growth etching the surface. The anterior end slopes somewhat more steeply than the posterior end causing the curvature to appear broadly rounded in the ventro-posterior region. The hinge-line is rather wide and straight. The provinculum is thin, raised, and lined with two rows of indistinct, minute, transverse tooth-like projections which fade and disappear on each side at some distance from the resilium (Fig. 1). The umbos are elevated, subconical, and while occupying the mid-dorsal portion of the valves, slant rearward to overlie the hinge-line. The left umbo is the more prominent. The size

(height) ranges from 0.22 to 0.32 mm. at the completion of the prodissoconch. The color is pale yellow to flaxen.

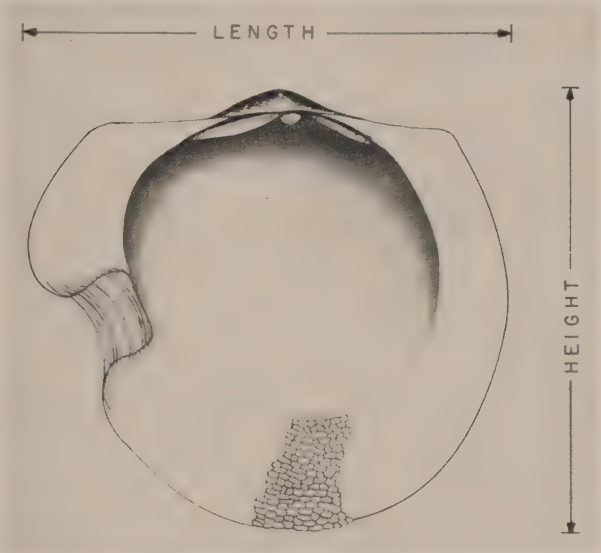

Figure 1. Line drawing of right valve showing dissoconch structure. Internal view. Height 0.5 mm.

THE POSTLARVAL SHELL

The changeover from a planktotrophic larval existence to a more or less stationary juvenile and adult life necessitates marked changes in the anatomy and shell formation of the sea scallop. These changes, modifications, and additions in the form and structure as seen at various stages in the progressive development of the shell can be brought out more clearly by a systematic description of each major character.

Shape and Color. The valves soon lose the equal convexity of the larval form, the top valve retaining a similar convexity while the bottom valve flattens considerably. The margins meet evenly until the young postlarval stages reach about 5 mm. in height when the valves begin to gape slightly but noticeably at each end in the dorso-lateral region. The gaping increases with size and is quite pronounced in adult specimens. The ventral margin is thin and simple with the upper valve slightly overlapping in

young specimens (Fig. 2). This feature remains constant during development except in some old specimens in which the edge thickens.

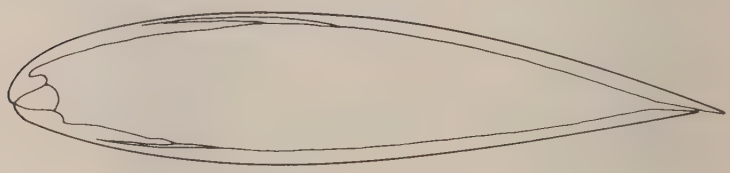

Figure 2. Line drawing of a specimen 17.2 mm. to show various structures of the shell in cross-section.

The form of the shell changes with growth. The prodissoconch is broadly rounded, slightly longer than high. The scallop continues to be slightly compressed dorso-ventrally until it reaches a size of 1 to 1.5 mm. at which time the height and length are about equal. The shell now gradually becomes more and more compressed laterally so that it is at its greatest extent in specimens between 70 and 90 mm. in height. Then the shell slowly begins to broaden again, and specimens 110 to 120 mm. assume a broadly rounded shape of similar height and length. The broadening of the shell continues and, in an average series, specimens larger than 120 mm. become increasingly longer than high. Individual specimens sometimes vary considerably but the measurements in Table 1 typify the general average of the sea scallop.

Table 1 — Ratios of height to length illustrating the changes in shell symmetry during growth

Height (mm.)		Length (mm.)	Ratio	Height (mm.)		Length (mm.)	Ratio
*0.072	x	0.088	1.22	78.3	x	73.1	0.93
**0.30	x	0.32	1.07	96.5	x	92.5	0.96
0.55	x	0.57	1.04	112.2	x	112.2	1.00
1.32	x	1.32	1.00	122.0	x	124.2	1.02
2.30	x	2.16	0.94	140.8	x	146.4	1.04
10.0	x	9.2	0.92	178.0	x	188.0	1.06
58.1	x	52.8	0.91	***208.0	x	230.0	1.11

*Straight-hinge veliger
**Completed dissoconch
***Largest scallop recorded in the literature (See Norton 1931)

Color pigment is lacking in the early dissoconch but when it reaches about 1.5 mm. a light cream tint develops. From this size on, color of various intensities ranging from light brown to dark reddish brown becomes increasingly prominent. Occasionally, albino, yellow, lavender, or radially dark- and light-rayed specimens are produced. Sometimes the color changes as the shell increases in size. Brown or reddish brown is the usual adult color. The under valve usually remains white or cream-colored throughout growth.

Shell Structure. The prodissoconch is thin and hyaline and continues translucent through the first few millimeters of growth of the postlarval shell. There is a complete change in the structure of the shell of the dissoconch. The larval shell with its high cuticular content is succeeded by the postlarval shell containing a high percentage of calcium salts. The shell is no longer simple; rather it becomes layered and more complex in structure.

As is well known, the periostracum, shell and ligament are products of secretion from the mantle. Outer and inner shell layers are formed in the dissoconch of *Placopecten* with color pigment being deposited in the outer layer. The periostracum and the outer shell layer are secreted by the lobes of the mantle edge with a resulting increment at the periphery. The general surface of the mantle is responsible for the secretion of the inner layer, the amount and regularity of which subsequently determines the shell thickness. The layers begin to form from the moment dissoconch growth commences. An additional layer, different in structure and composition, is formed by the modified mantle epithelium of the adductor muscle. This layer is seen to fracture on a vertical plane with respect to the shell surface. It is difficult to make out any microscopic features in this layer without using special techniques because of the homogeneity and transparency of the substance. In *Pecten*, according to Böggild (1930), this layer is prismatic in structure and the prisms are very thin, straight, regular, and oriented to a vertical axis. Böggild found (using certain techniques of refraction) that this layer is aragonitic as opposed to the calcitic outer and inner layers. The layer is first apparent in the sea scallop at about 2 mm. The outer layer is thin and only clearly visible in sectioned shells 15 mm. or less in size while the inner layer is much thicker and can be seen in all sizes. The inner layer is built up of irregular parallel leaves to appear as a foliated structure.

Figure 2 shows a transverse section of a juvenile sea scallop

of 17.2 mm., drawn with the aid of a camera lucida. Of interest is the relative thickness of the valves, the amount of overlap of the upper valve at the ventral margin, the position of the upper and lower muscle scars, and the arrangement of the hinge and ligament. Of particular interest is the method of development of the layer produced by the muscle epithelium. The adductor muscle must necessarily change position as the shell enlarges in order to maintain a somewhat central location. This is accomplished by a ventral migration of the muscle. At the same time deposition of shell material continues in the area contiguent to the muscle so that in time a distinct middle layer dorsal to the muscle is produced.

A well-defined prismatic layer is easily seen in the lower valve of the young dissoconch when viewed from above (Figs. 1 and 3; Pl. 2, fig. 2). The prisms are irregularly shaped and are secreted

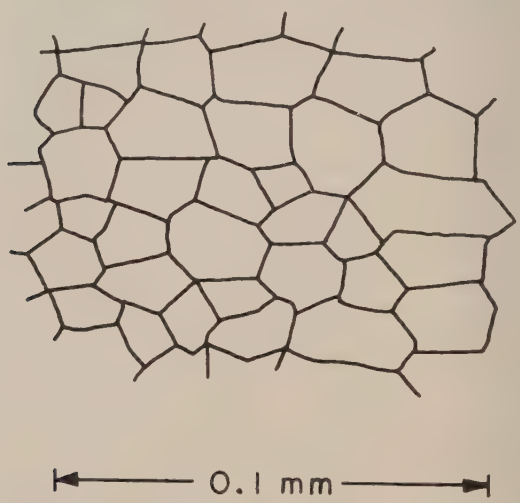

Figure 3. Line drawing to show prismatic structure in the right valve.

in an erratic, though concentric pattern. On the average, when measured near and parallel to the ventral margin, there are about 5 prisms per 0.1 mm. The prismatic pattern persists until the shell reaches about 5 to 7 mm. in height at which size the shell becomes too thick for this structure to be seen clearly.

The External Sculpture. The surface sculpture differs in the

two valves. In the upper valve, commencing with the onset of dissoconch growth, microscopic radial ridges develop which are crossed at intervals by similarly delicate concentric ridges which result in a sharply defined cancellated or nodulated sculpture. At about 2 or 3 mm. the concentric ridges weaken and gradually disappear whereas the fine radial ridges are retained. Shortly thereafter heavier raised primary ribs begin to radiate regularly among the intervening microscopic ridges which in turn fade and cease to be produced in juvenile specimens between 10 and 20 mm. The fine ridges may be straight and regular or they may be vermicular or oblique in which case they usually cross the ribs. This is the "camptonectes" sculpture of Verrill (1897). Commencing with the juvenile, the regularly spaced primary ribs are a prominent part of the upper valve, new ribs being added between them as the shell enlarges (Pl. 3). When they first appear, the ribs are spaced about 0.3 mm. apart. When the spacing increases to 0.8 to 1.2 mm., a new rib is added. The distance between the ribs increases as the shell size increases until in the adult stage the ribs are spaced about 1 mm. apart. The ribs of the adult may be strongly raised and serrated causing the shell to look and feel rough, or, in the case of a smooth-shelled adult, the ribs may be but slightly raised.

Any concentric markings beyond that mentioned for the early dissoconch are in the form of numerous fine laminal lines (striae) as the result of frequent additions during growth. At intervals these lines of growth become more closely spaced appearing as thickened bands of shell material. Stevenson and Dickie (1954) and most present-day investigators working with the sea scallop believe that the more prominent bands are caused by the seasonal changes of growth pattern, as has been demonstrated with the annual rings of trees or fish scales.

Radial sculpture is formed somewhat similarly in the bottom valve. However, due to the formation of prismatic structure in the early dissoconch the fine ridges do not start forming until the shell is about 5 to 7 mm. in height. Primary ribs soon develop as in the upper valve but not as strongly. Although both the ribs and ridges usually persist through to the adult, either or both may disappear during the course of development. If the sculpture persists it is weaker than in the upper valve.

The radial sculpture of the wings is similar to that on the surface of the shell, but it is usually more strongly developed, especially so in the anterior wings (Pl. 3). Concentric sculpture

ending at the wing margins forms crenulations at the hinge line.

The Inner Shell Surface. The mantle is attached to the shell by a series of muscles along the pallial line. The mantle is able to expand and retract from this line to the outer edge of the shell. In the adult the surface area outside the pallial line appears smooth and lustrous to the eye but upon closer examination flakey laminal

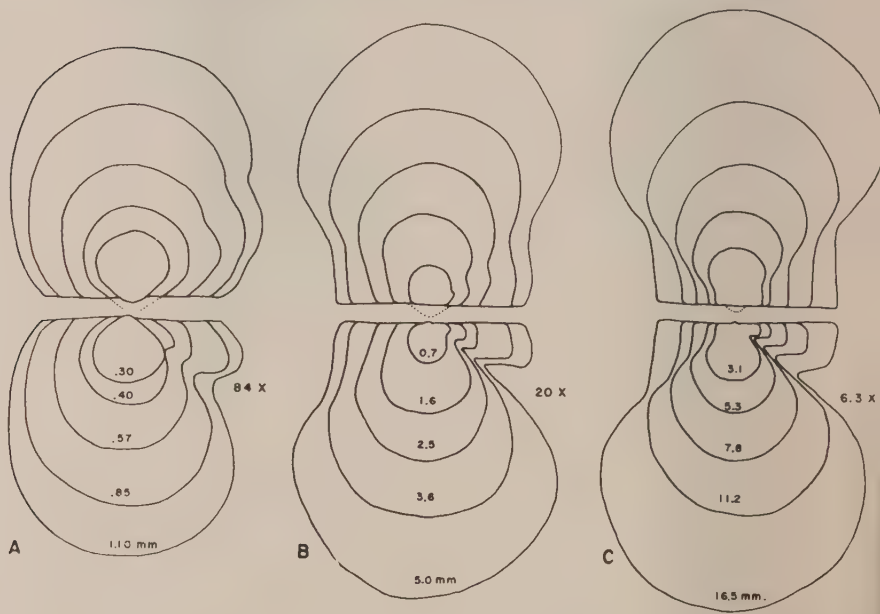

Figure 4. A series of line drawings showing the development of the wings of the sea scallop.

layering can be observed, particularly near the margin. Also, very fine lines radiate to the margin. Within the pallial line, the calcium deposits appear nacreous with coarse and irregular layering. The adductor muscle scar is large, distinct, and, particularly on the right valve, placed off center toward the posterior border. The scar on the left (upper) valve is the larger and there is a line showing the separation of the muscle into a large anterior and a small posterior part. Within the scar, lines denoting the attachment of individual bundles are evident. The adductor muscle is attached to the valves somewhat more dorsally

and posteriorly in the young especially in the right valve, but it gradually moves to a more central location with increase in shell size, and after about 50 mm. advances proportionally to the ventral margin of the shell. The muscle scar forms a slight depression and is surrounded by the crystalline substance. The peculiar crystalline structure within the pallial line is first evident in the upper valve at about 2 mm. but soon can also be seen in the thinner bottom valve.

The Auricles or Wings. Figure 4 compares the outline of specimens in a series ranging in size from 0.3 to 16.5 mm. in height. These were specifically drawn to show the development of the wings. As can be seen, the settled prodissoconch lacks them. The earliest indication of their development appears in specimens which have put on just a fraction of a millimeter of dissoconch growth. A notch develops in the lower valve at the anterior margin, the portion of the newly-formed shell dorsal to the notch consequently appearing ear-like. The wing becomes broadly rounded as the height increases to about 2 mm. It now begins to angulate (Fig. 4b) and continues until the shell is about 10 mm. in height when the angle again broadens (Fig. 4c). The angle becomes less acute as the shell size increases so that in the adult this wing is more nearly symmetrical with the posterior one.

The development of the anterior wing in the upper valve proceeds in a peculiar fashion. A rounded flap begins to develop almost immediately, projecting over and overlying the byssal notch. Although fully developed at 1 mm., it persists through growth to nearly 5 mm.

At the same time as these wing-like processes are developing, slight indentations or depr ssions begin to form between them and the body wall. These are the slopes or submargins, the points where the wings can be distinguished from the body proper.

The posterior wings begin to develop at about 2 mm. and, with increase in size, slowly become more strongly outlined as the posterior submargins strengthen. The wings are easily distinguishable before 5 mm., becoming even better developed as the shell size increases. However, it is interesting to note that the ears are proportionally smaller in larger specimens. At 2 mm. the width of the hinge-line is about four-fifths the length of the shell, at about 35 mm. only about one half, and thereafter very gradually decreasing. The shell measurements in Table 2 clearly show this characteristic.

Table 2 — Width of hinge-line compared to length showing the decrease in the wing width in relation to length with growth (in millimeters)

Height	Length	Width of hinge-line	$\frac{\text{Width of Hinge-line}}{\text{Length}} \times 100$
1.9	1.8	1.5	83.3
5.8	5.2	3.8	73.1
10.5	9.1	6.3	69.2
21.3	18.9	11.6	61.4
34.6	31.6	16.2	51.3
52.3	48.0	20.8	43.3
106.8	104.2	44.3	42.5
142.6	147.7	62.0	42.0

Hinge-Plate. In young specimens the hinge-plate is thin, raised, and with a simple ligamental groove below the margin which is separated by an internal resilium (Fig. 5). The indistinct transverse teeth present in the prodissoconch cease to develop in the

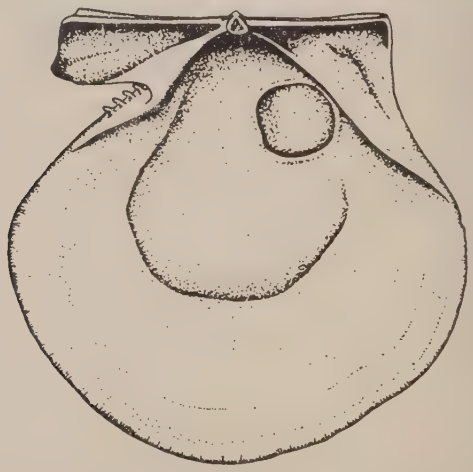

Figure 5. Line drawing of right valve of a specimen 5.7 mm. showing hinge-line and other internal characters.

early dissoconch. As the hinge-line develops, deposition of new material obliterates the larval teeth at about 0.5 mm. The hinge-plate, only slightly differentiated in the very young, becomes increasingly raised along the exterior margin as the shell develops

and this is directly responsible for the greater gaping of the valves in the dorsolateral region. At the hinge-line, the exterior margin is crenulated and recurves inward to impinge on the hinge-plate and partly overlap the ligamental groove. This becomes more apparent with increased shell size.

The Byssal Notch. Formation of the byssal notch commences at the moment of dissoconch growth. In the early dissoconch, little shell material is deposited in the lateral region of the under valve where the notch is located; instead, a rounded indentation is produced. With increase in size the notch advances accordingly as shell material is deposited behind it (Fig. 1). This material is not prismatic as is the rest of the valve in the early dissoconch; rather it appears homogeneous and hyaline, with laminated, concentric growth lines running parallel to the notch. As the shell enlarges and the notch continues to advance, a ridge is produced along the anterior submargin above which a groove has been excavated. A number of pectinidial teeth develop along the ridge. Teeth begin to form at a size of about 1.5 mm. (Pl. 2, fig. 2) and cease after about 25 mm. Occasionally, the teeth are feeble or may not develop at all. In one specimen over 30 teeth were counted. Plate 3, figure 1 illustrates a 5.7 mm. specimen in which 15 teeth are present. The early-formed teeth can usually be observed in the adult well back on the raised ridge in the vicinity of the umbonal region unless erosion or calcification has destroyed or covered them. The notch is broad and rounded inside for the first millimeter or two (Fig. 1) but soon begins to angulate as the wing develops. After a size of 10-15 mm. the angle becomes gradually less acute (Pl. 3, fig. 3) as the notch fills in so that in the adult the notch is almost entirely obliterated.

The Ligament. The structure, function and mechanical properties of the ligament in *Pecten* have been fully described and discussed by Trueman (1953a, b). Briefly, the ligament joins the two valves of the shell together dorsally along a hinge-line and functions by working in opposition to the adductor muscle, thus forcing the valves to gape apart when the muscle is relaxed. There are two layers, the outer which extends thinly along the dorsal margin of the valve hinges, and the inner which is centered immediately below the hinge at the umbo. A thin layer of periostracum is produced over the outer layer. The layers are laminated and, according to Trueman (1953a), composed largely of tanned proteins, an organic matrix commonly referred to as "conchiolin."

The inner layer, or resilium, is triangulate in shape, its apex coincident with the umbonal point of the valves. It is housed in a depression, the resilifer, the base of which projects shelf-like into the cavity of the shell. It is composed of three parts: a large central region consisting of amorphous, non-calcareous tanned proteins, brown in color and of a rubbery consistency, and two small lateral calcified regions in the area of attachment to the resilifer.

In the early postlarval shell of the sea scallop the outer ligament lines the hinge as a very thin, transparent substance. As the shell enlarges this layer becomes increasingly conspicuous principally because the brown color in it is darker.

In the larval shell of *Pecten* the ligament is situated internally and off center on the straight hinge toward the posterior broad end of the larva (Rees, 1950). In the recently settled larva of the sea scallop the resilium is about centered between the umbos (Fig. 1). It is wide and rounded, and seated within a weakly developed resilifer. After the first millimeter of growth the resilium begins to lengthen and soon takes an almost equal-sided pyramidal shape as new ligamental material is added ventrally and laterally. After 5 mm. (Fig. 5) to 10 mm. the resilium gradually begins to elongate in a dorso-ventral direction until in the adult it is long and slender. The resilifer strengthens with growth, the depression gradually deepening so that in the adult the resilium is deeply rooted.

The ligament, formed by secretions from the mantle, is subject to the same general growth and shock lines as is the shell. Less prominent impressions are found in the tanned protein portion than in the calcified outer portion of the inner ligament.

DISCUSSION

The major changes during the development of the shell of the sea scallop have been described in the preceding pages, thus serving the primary purpose of this paper. However, the subject would not be complete without a brief discussion of certain points described elsewhere.

The D-shaped veliger shell is usually distinctly marked off from the umbo veliger stage in most species (Rees 1950). This is not the case with the sea scallop. Apparently there is little or no cessation of growth during larval shell development to cause this distinct line to be formed. Thus, the early veliger is almost impossible to identify in the plankton. Also the size at this stage

varies considerably and is of little use as a character. This agrees with Jörgensen's (1946) findings regarding the reliability of the length of Prodissoconch I ["straight-hinge" stage] as a specific criterion. Of course, by the time of development to the umbo stage this species should be identifiable through hinge characters. Stafford (1912) states that larval sea scallops are easily identified because of their equal measurements in length and depth. Of the scallops examined in this study, the length commonly exceeded the height in the prodissoconch. Stafford also speaks of a notch that may appear in front of the median point of the margin, which soon develops into two little beaks on the left valve, and a larger interlocking tooth on the right valve. Borden (1928) also remarks on this occurrence but it is quite possible she simply followed Stafford's earlier work. No such anomiaiid-like character was observed in any of my specimens. In fact, I should be very much surprised if such a character existed in this species, principally because it is not a known phylogenetic character in the Pectinidae.

The prismatic structure in the under valve of the early post-larval sea scallop has been described elsewhere in this paper. In very young specimens the margin of this valve is very thin and flexible due to the organic matrix bordering each prism. Similar prismatic structure can be seen in other species of the Pectinidae, and is especially prominent in thin-shelled deep-water forms. Carpenter (1847, p. 95) first observed this character in *Pecten nobilis*. The flexibility of the under valve allows the shells to compress snugly together when necessary and seems to serve essentially to give extra protection.

The very young sea scallop puts out a short branching byssus which allows it to adhere closely to the surface to which it attaches. The rounded flap that precedes the development of the anterior wing overlies the byssal notch and appears to function as a protective lid in the young dissoconch. Thus when a young scallop is disturbed it squeezes its valves tightly together and, being attached close to the surface with its attachment protected, is better able to withstand and survive the early vicissitudes of life.

Before leaving the subject of byssal formation, it is of interest to note that the sea scallop retains the habit of byssal fixation for some time after reaching adult size. I have measurements of scallops as large as 112 mm. in height which were found still attached to rocks. The scallop does not remain attached all of

this time. It frequently breaks away and swims about for a time before attaching again.

It should be noted that Dall (1886, pp. 207, 222) and Verrill (1897, p. 79) both described well-developed transverse incisions on the hinge-plate in young sea scallops as did Jackson (1890). I have not been able to detect any signs of transverse grooves or ridges in this species other than the very indistinct transverse tooth-like projections in the larval shell which fade and disappear very shortly in the dissoconch and which are invisible unless the specimen is properly prepared and mounted. Apparently the above authors, like Jackson, had the young of other species before them when they described this feature.

Dall (1889) discusses the radiating ridges or ribs found in certain groups of pelecypods and concludes that they serve to add strength to the shell while not increasing the weight as would a corresponding increase in thickness of the shell. As it happens. the adult sea scallop increases the thickness of the shell rather than develop strong radial sculpture. However, the young scallop of 5 to 30 mm. (Pl. 3) has rather strong ribs which would tend to strengthen the shell before it has had a chance to thicken markedly. The radiating ribbed sculpture of the wings is particularly strong. The wings at these sizes are proportionally wider at this early age but thin, and the extra strength is desirable in this area of the pivotal axis of the valves where there are mechanical stresses and reactions of one valve upon the other for the scallop to contend with.

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PLATES

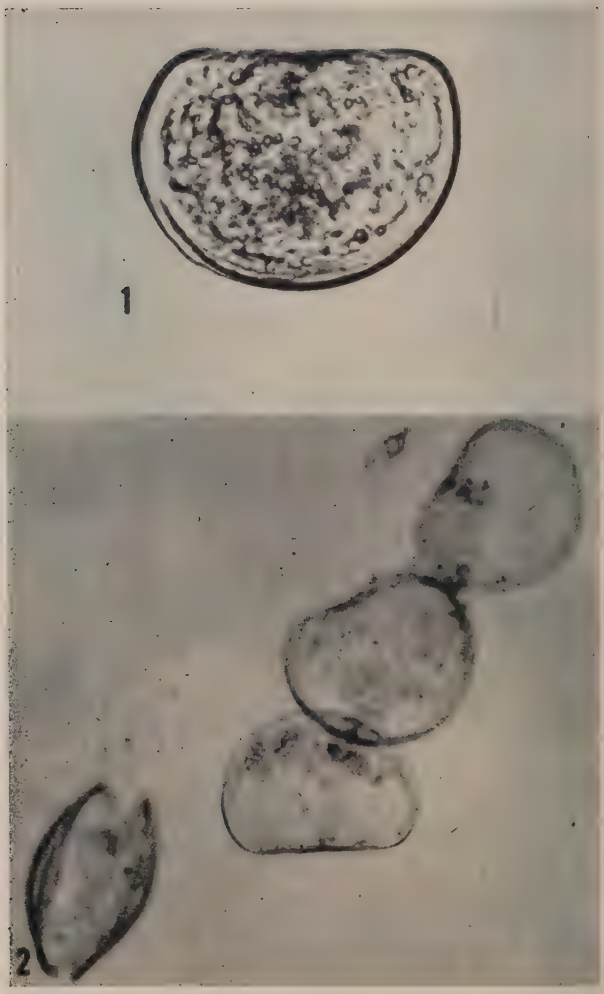

PLATE I

Figure 1. Seven-day-old laboratory-reared sea scallop in the straight-hinge stage. Animal within shell (about 300X).

Figure 2. Same as Figure 1. Shell valves only (about 500X).

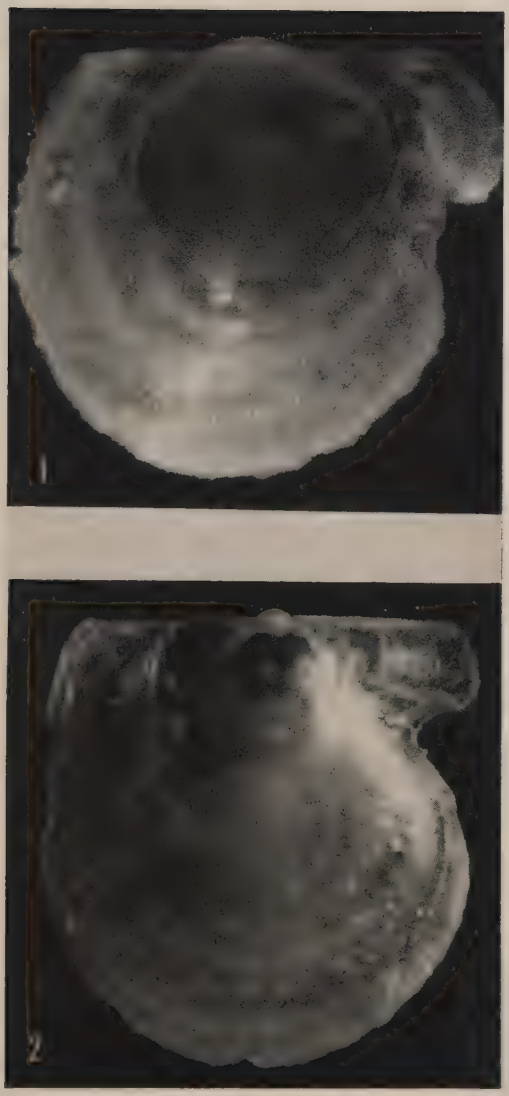

PLATE 2

Figure 1. Right (bottom) valve of early postlarval sea scallop. Height 0.5 mm.

Figure 2. Right valve showing first pectinidial tooth. Height 1.5 mm.

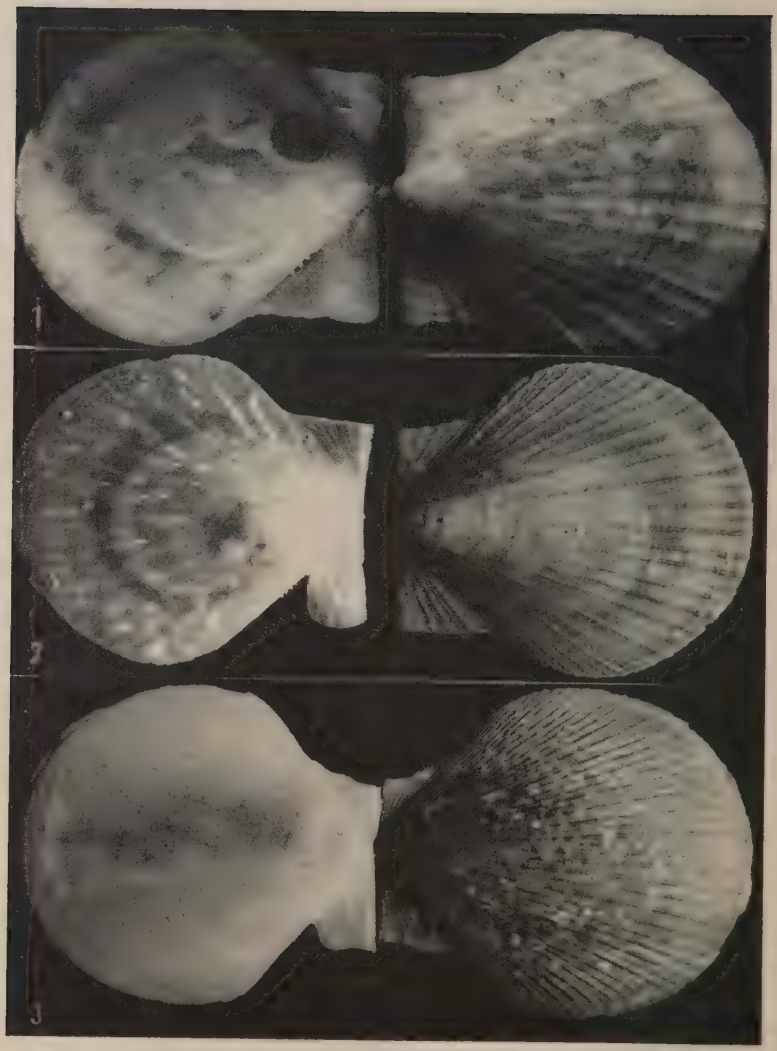

PLATE 3

Figure 1. Left and right valve of a specimen 5.7 mm. in height (both valves doubled).

Figure 2. Left and right valve of a specimen 11.7 mm. in height.

Figure 3. Left and right valve of a specimen 20.5 mm. in height.

THE SEA SCALLOP FISHERY

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Woods Hole, Mass.

(Abstract)

An important year-round fishery for the sea scallop, *Placopecten magellanicus* (Gmelin) is carried on along the Atlantic coast. This scallop is fished commercially from off Prince Edward Island southward to offshore in the area of Cape Henry, Virginia. However, most of the total catch is taken in the relatively limited area of Georges Bank, off Massachusetts, by United States and Canadian scallop fishermen. The scallops are shucked at sea, the meats bagged, iced, and stored below deck until return to port. Most U. S. vessels land and auction their scallops at New Bedford, Massachusetts. Over 200 million pounds of meats (about 6 billion scallops) have been taken from Georges Bank by the New Bedford fleet from 1945 through 1960. In 1960 total landings exceeded a record 32.4 million pounds.

In 1954 a program was established by the Bureau of Commercial Fisheries Biological Laboratory at Woods Hole, Massachusetts, to investigate the sea scallop fishery. Here vital statistics of the fishery, collected from interviews at key ports along the coast, are processed and analyzed. Basic data are collected by periodically surveying and sampling the scallop grounds with a research vessel. These data are used to determine the potentially productive grounds and to predict the strength of pre-recruit year classes. An essential part of the program is an understanding of the population dynamics of the fishery. This necessitates studies in growth and mortality rates, and mesh selection experiments with the scallop dredge. Studies in basic biology include several diverse enterprises such as culturing larvae and collecting spat for early life history studies, time and cause of formation of annual rings, seasonal cycle of gametogenesis and spawning, and seasonal and areal variation in length-weight ratios.

Our studies to date have led recently to a request through the International Commission for the Northwest Atlantic Fisheries for a regulation to increase the ring size in the mesh of the scallop dredge from 3 inches to approximately 4 inches, the exact size is yet to be determined. This will effectively postpone capture of small scallops for about a year. The increase in meat weight will more than offset the loss by mortality thereby increasing the total meat yield to the fishery.

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A MODIFICATION OF THE SMALL HARDY PLANKTON SAMPLER FOR SIMULTANEOUS HIGH-SPEED PLANKTON HAULS

BY

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Introduction.

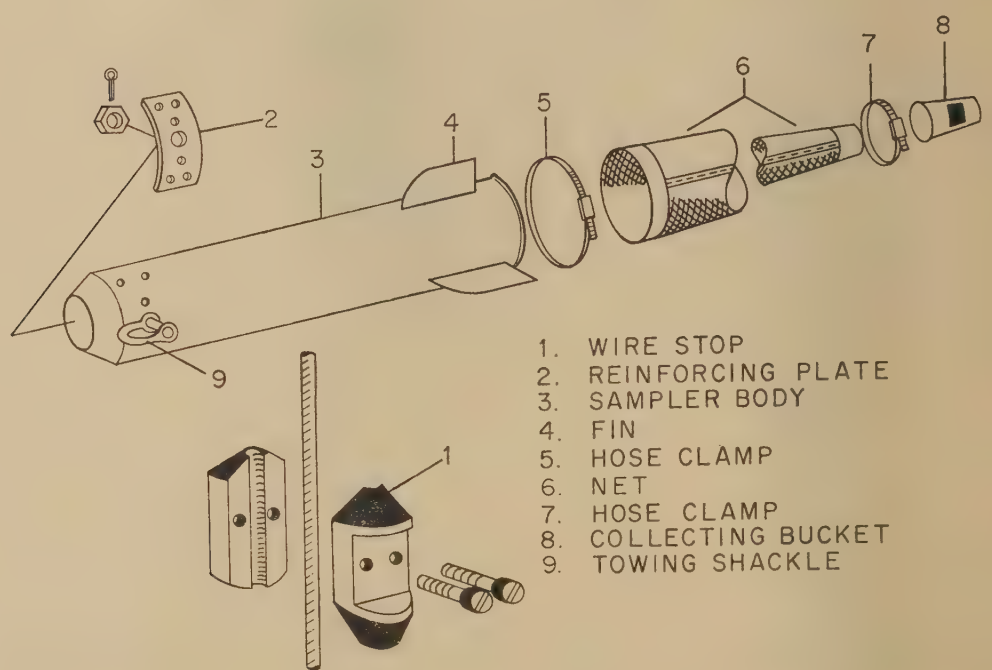
In 1953, an investigation of the distribution and relative abundance of haddock eggs and larvae in the Gulf of Maine and Georges Bank was begun at the Woods Hole Biological Laboratory of the Bureau of Commercial Fisheries, United States Fish and Wildlife Service. The initial phase of this programme was an assessment of the horizontal distribution of these eggs and larvae over the broad area under consideration. As an outgrowth of this programme, a study of the vertical distribution of the haddock larvae, within areas where they were concentrated, was proposed. One of the first problems encountered in planning for this second phase was the selection of suitable sampling gear. To this end, criteria for sampling gear which would meet the specific requirements of such a programme were proposed as follows :

Simultaneous samples from a number of strata : This seemed to be the most logical method of accurately sampling the vertical distribution of planktonic forms.

Simplicity of design and construction : The design was to be as simple as possible in order to minimize original cost, avoid breakdowns in use, and permit ease in operation.

High towing speed : Towing speeds in excess of 5 knots were planned in an attempt to reduce, as much as possible, the effects of escapement.

High filtering ratio : The ratio of effective filtering area to aperture was to be sufficiently large so that the effects of clogging would be minimized, and a high rate of flow maintained under all sampling conditions.



TEXT-FIG. 1.—Detail of sampler.

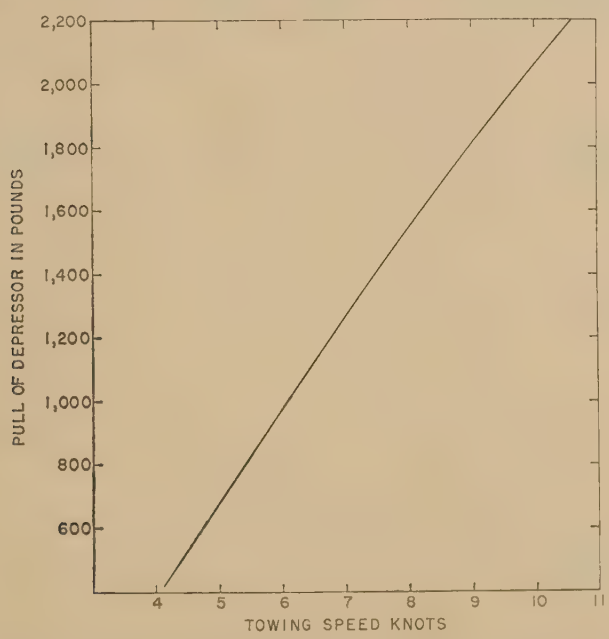
Adequate sampling aperture : In assessing changes in the vertical distribution of organisms with time it is important to make tows of short duration at frequent intervals. Thus, a sampling aperture large enough to admit a reasonable volume of water during a short tow was essential.

Absence of obstruction to the sampling aperture : It was felt that the sampling aperture should be clear of obstruction and be located in advance of the towing wire.

The device most closely fulfilling these criteria was the small Hardy plankton sampler described by Glover (1953). The sampler herein described is based on Glover's design, reworked to fit our specific needs. It is to the greater credit of the original design that this modification has proved so successful in use.

Description of the Gear.

The entire sampler body is constructed of fibre-glass (six layers of glass cloth bonded with an epoxy-resin) ; this material is strong, light in weight, and is particularly resistant to fatigue resulting from vibration. The component parts and details of assembly are shown in Text-fig. 1. The body tube is 24 inches long, with an internal diameter of $5\frac{1}{2}$ inches, and is fitted with a tapering nosepiece, reducing the sampling aperture to 4 inches. The wall thickness is approximately $\frac{1}{8}$ inch. Three stabilizing fins are located symmetrically at the rear of the body tube. The sampler is towed from a $\frac{3}{8}$-inch bronze shackle, with spring-loaded



Text-fig. 2.—Pull of 60-pound multiplane kite otter at various towing speeds with 200 metres of $\frac{1}{4}$-inch wire.

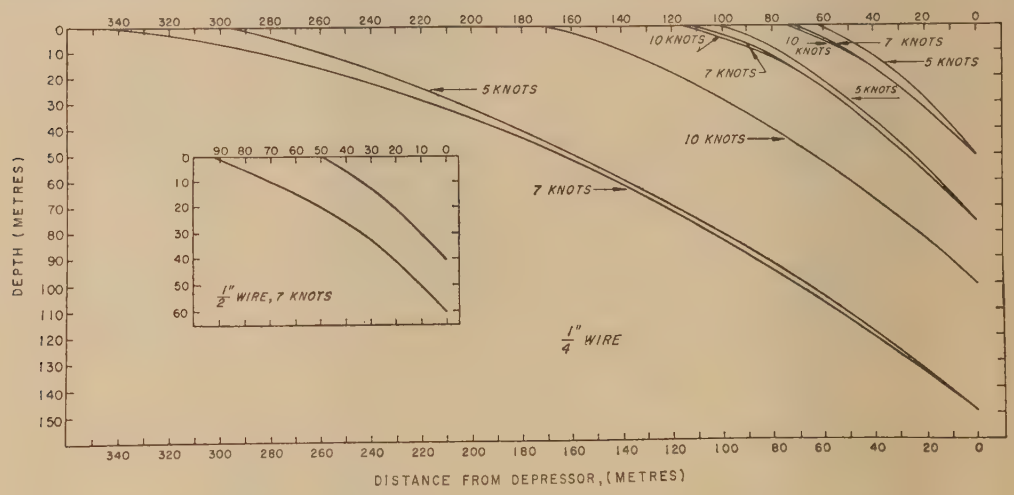
catch, fastened to the left side of the body, 4 inches behind the aperture. A $\frac{3}{8}$-inch stainless steel bolt, threaded into a $\frac{1}{8}$-inch brass reinforcing plate located inside the body tube, supports the towing shackle. Brass wire-stops on the towing wire support the sampler so that it is free to rotate about the wire and thus be properly orientated to the direction of flow when under way.

A nylon collecting net 36 inches long, tapering from $5\frac{1}{2}$ inches in diameter at the forward end to 3 inches at the terminal end, is fastened to the rear end of the sampler body by a screw type stainless steel hose clamp. A conventional brass collecting bucket provided with two screened apertures is fastened to the after end of the net with a stainless steel hose clamp. The total weight of the sampler,

including the nylon net and bucket is 5 pounds. A wire mesh net wholly contained in the sampler body has been experimented with. This net added significantly to the cost of the samplers but seemed to offer no particular advantage over the external nylon net described.

The U.S. Navy Type "O", 60-pound multiplane kite otter described by Colton (1959) is used as a cable depressor. This depressor has excellent diving characteristics and should see wider use in marine research.

Since the practical depth which can be attained is dependent partly on the wire diameter, $\frac{1}{4}$ inch wire is recommended for the towing cable. We have used



TEXT-FIG. 3.—Curves for determining sampler spacing on $\frac{1}{4}$-inch wire with the kite otter at 150 metres (towing speed 5 and 7 knots), 100 metres (towing speed 10 knots), 75 metres (towing speed 5, 7 and 10 knots) and 50 metres (towing speed 5, 7 and 10 knots) and for $\frac{1}{2}$-inch wire with the depressor at 40 and 60 metres (towing speed 7 knots).

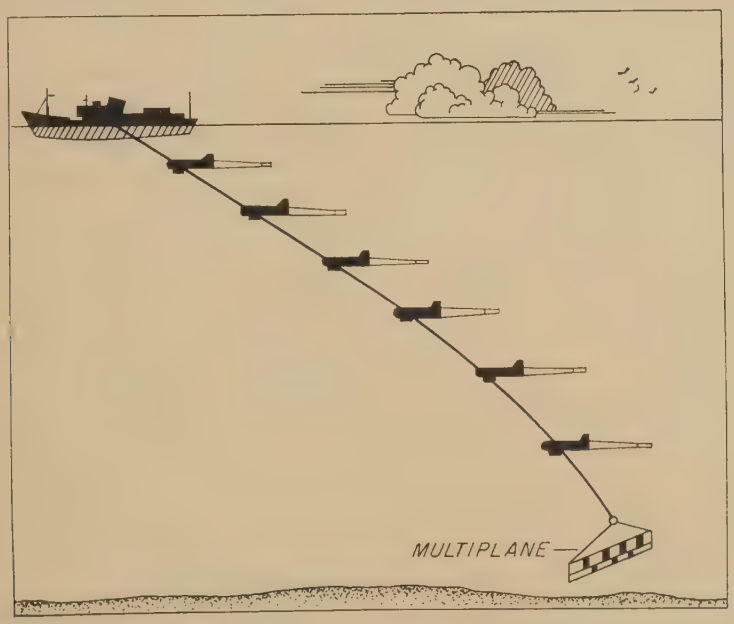
7×19 galvanized air cord and had no wire failures in some 50 hours of towing. The results of a series of trials to determine the pull exerted by the depressor in actual use are summarized in Text-fig. 2. The figures for the wire pull used in Text-fig. 2 are average ones. Trials were made with a moderate sea running, and the dynamometer readings tended to rise and fall over a range of about 500 pounds with the motion of the vessel. The absolute maximum reading obtained during the trials was 2500 pounds at a speed of 10 knots with 200 metres of wire out. The average pull of the depressor when operating at this speed was only 2100 pounds. Since the rated breaking strain of the wire specified is 7000 pounds (a minimal figure provided by the manufacturer) there is a safety factor of about three at this speed. This is somewhat less than the recommended factor of five. For our own work, a towing speed between 7 and 8 knots has proved to be ample. In this speed range the tow load is reduced to about 1500 pounds, providing a safety factor

close to the figure recommended by the manufacturer. Regardless of the towing speeds used, common sense safety precautions should be observed.

In rigging the gear aboard the vessel, sheaves of a width sufficient to pass the wire-stops should be employed. This obviates the removal of the wire-stops at the beginning and end of the tow.

Operation of the Gear.

The absence of a metering device in the samplers places certain limitations on their use. Sub-surface currents will introduce considerable error between samples collected at different depths. Unless a suitable metering device is employed, the



Text-fig. 4.—Schematic representation of sampling gear under tow.

homogeneity of the water column in terms of lateral transport should be determined, so that the samples for each depth are volumetrically comparable.

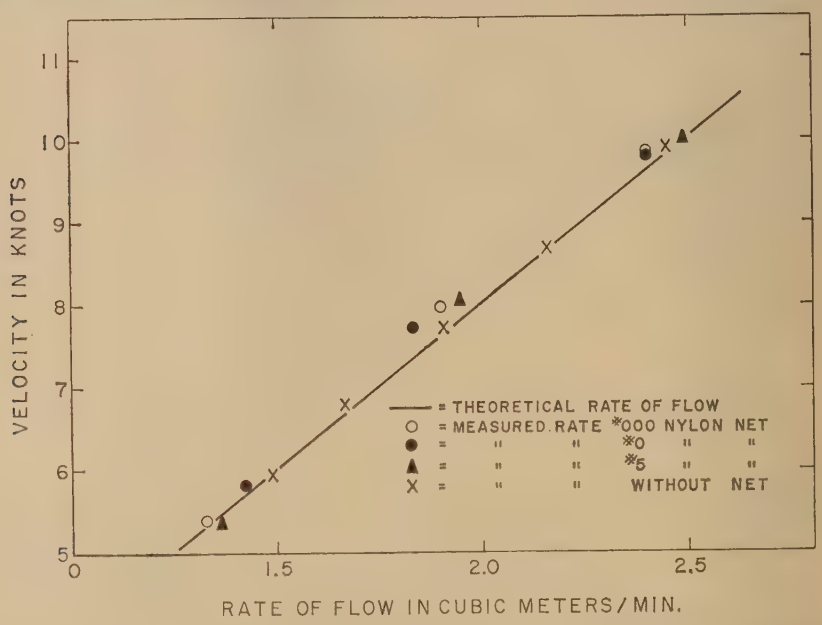
In a replicate series of tows, changes in ship's speed due to changing wind and sea conditions introduce error between tows. To minimize this source of error, tows should be made over a circular course. A drifting buoy with drogue will serve as a reference point for such a series of tows and in addition, locate the water mass being sampled.

Once the specific depths to be sampled have been decided upon, the proper spacing of the samplers on the towing wire can be determined by referring to Text-fig. 3 (redrawn from Colton, 1959). It is most convenient to set the gear with the

vessel either standing or moving ahead very slowly. The wire is paid out slowly and the samplers attached while running the wire out. When the proper amount of wire has been set, the vessel is then brought promptly to towing speed. At the completion of the tow, the ship is stopped as rapidly as practicable and the gear retrieved. Text-fig. 4 shows a general view of the gear in operation.

Filtering Capacity of the Sampler.

A series of calibration trials was made by the U.S. Department of Commerce National Bureau of Standards (Capacity, Density, and Fluid Meters Section) to



Text-fig. 5.—Filtering capacity of sampler at various rates of flow; for details, see text.

determine the capacity of the samplers at various rates of flow and also to determine the effects of several net sizes and mesh sizes on the rate of flow. Nylon nets of three mesh sizes were used: No. 000 (0·947 mm.), No. 0 (0·526 mm.), and No. 5 (0·263 mm.). These nets provided an 18 : 1 ratio of effective filtering area to sampling aperture, the ratio varying only slightly with mesh size. Each net was tested with the collecting bucket placed at the end and near the $\frac{3}{4}$, $\frac{1}{2}$, and $\frac{1}{4}$ points of its length to simulate the effects of clogging. A condensation of the results of these tests is given in Text-fig. 5. The results of these tests show that very nearly the same amount of water flows through the sampler, no matter which net is used, how much it is clogged, or how fast it is towed over the range of speeds tested.

These results do not differ greatly from the computed theoretical capacity. Thus quantitative figures computed on the basis of the theoretical filtering capacity would seem to be sufficiently accurate for most work.

Sampling Errors.

In sampling simultaneously at various levels with the gear herein described, it is obvious that the surface sample is the only one taken wholly at its intended level. The instrument intended to sample at some lower level, let us say 30 metres, travels from the surface to some depth exceeding 30 metres as it is set, then returns to 30 metres as towing speed is reached. At the termination of the tow, it again drops below its proper level and from that point is hauled to the surface. The error incurred is then the total volume of water filtered during the haul, divided into that volume of water taken at levels other than 30 metres. This error increases with the depth sampled, so that the deepest running sampler is subject to the greatest error. Since the general order of magnitude of this error is of some importance here, its theoretical value has been computed for several depths and speeds; the results are listed below. These computations were made on the basis of a 30-minute tow, the volume filtered being 0·0081 m.^{3} per metre of tow.

Total length wire used (metres).	Maximum depth sampled (metres).	Speed of tow (knots).	Error in percent of total volume sampled.
345	150	7	14
160	100	7	6
170	100	10	5
112	75	7	4
116	75	10	3
73	50	7	3
75	50	10	2

At depths of 100 metres and less, that percentage of the tow taken outside the desired sampling depth is a small one. At a depth of 150 metres, however, the error may be important. In sampling at sea, however, this error is no doubt substantially smaller than that indicated here, since the above values assume that the gear operates as efficiently while being raised and lowered as it does under tow. This assumption would appear to be invalid, at least regarding the more active planktonic forms.

The modified Hardy samplers may be obtained from Mr. Fred Schueler, 30 Albemarle Road, Waltham 54, Massachusetts, U.S.A.

Some Results.

Subsequent to field testing, these samplers were used in a study of the vertical distribution of haddock larvae. Although the results are the subject of a separate paper, currently in preparation, certain aspects of the data relating to the effective-

ness of the samplers are included here. Tows of 30-minute duration were made around a free drifting marker buoy, simultaneous samples being taken at depths of 1, 10, 20, 30, 40, and 50 metres. Each of three stations was occupied continuously for 48 hours. The general condition of the collected material was excellent. It was not unusual, when preparing catches for preservation, to find a major proportion of the invertebrate zooplankton forms alive. Fish larvae were more susceptible to damage yet less than 1% were damaged to the extent that identification was impossible.

Of fundamental importance is the fact that the data showed very little difference between day and night catches of haddock larvae. Further, these differences remained consistent throughout the range of sizes taken (4–21 mm.), indicating that escapement of the larvae, insofar as it relates to changes in both light intensity and swimming ability, is virtually eliminated when the gear is towed at speeds of 7 knots. An examination of the collections for invertebrate zooplankton indicated a species composition which compared favourably with data from metre net collections made in the same general area. Notable exceptions, however, were the more active planktonic forms such as euphausiids, hyperiid amphipods, and pandalid shrimp which occurred more often in the high-speed samplers than in the metre nets.

Based on the experience of actual field use, the entire sampling equipment has proved extremely effective in assessing the vertical distribution of planktonic forms within its prescribed limitations.

Summary.

1. A high-speed plankton sampler specifically designed for the study of the vertical distribution of larval fish is described, and the method of its operation noted.

2. Tests indicate that the filtering capacity of the sampler is relatively constant with several mesh sizes and over a range of towing speeds from 5–10 knots.

3. Estimates of the sampling error introduced by the difference in volume strained between the surface and deeper samplers are given. The estimated values of these errors appear to be well within acceptable tolerances for biological data.

4. The samplers have been used effectively in a study of the vertical distribution of haddock larvae. Results of this study indicate that the daytime escapement of active zooplankton forms generally encountered in the use of slow-moving nets is virtually eliminated.

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Incidence of the Giant Trematode, *Hirudinella marina* Garcin, in Skipjack Tuna, *Euthynnus pelamis* (Linnaeus), from Marquesan and Hawaiian Waters

Eugene L. Nakamura and Heeny S. H. Yuen

Incidence of the Giant Trematode, *Hirudinella marina* Garcin, in Skipjack Tuna, *Euthynnus pelamis* (Linnaeus), from Marquesan and Hawaiian Waters[1]

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ABSTRACT

The greater incidence of the giant trematode, *Hirudinella marina* Garcin, in skipjack tuna, *Euthynnus pelamis* (Linnaeus), from Hawaii than in skipjack from the Marquesas led to the hypothesis that this difference in infestation was due to area. Comparisons with respect to sex, size, and time led to the conclusion that a major source of variation could be attributed to time. The available data did not allow a conclusion on whether or not a real difference exists between the two areas.

INTRODUCTION

During 1956 and 1957 the staff of the Honolulu Biological Laboratory, U. S. Bureau of Commercial Fisheries, conducted an investigation of the response of skipjack tuna, *Euthynnus pelamis* (Linnaeus), to live bait in the region of the Hawaiian Islands (Yuen, 1959). During 1957 and 1958 a survey was made of the "surface" tuna resources in the region of the Marquesas Islands in northeastern French Oceania. Studies of stomach contents of skipjack tuna were important to both of these investigations. While examining the data, it was noticed that the incidence of the giant trematode, *Hirudinella marina* Garcin, was apparently considerably higher in skipjack stomachs from Hawaii than in those from the Marquesas. Analyses of the data, however, revealed no conclusive difference in infestation rates between these two areas. The results of analyses showing differences associated with other factors such as size, sex, and time are presented below.

METHODS

Stomach samples were collected from skipjack caught by the live-bait method (June, 1951). The stomachs were removed intact and placed in white muslin bags with appropriate labels and then placed in 10-percent formalin. Stomachs distended with food were slit in order to facilitate preservation. Field data included the time and locality of capture, total length (as defined by Marr and Schaefer, 1949), and the sex of the fish.

Sampling in the Marquesas was carried out from U. S. Bureau of Commercial Fisheries' research vessels. From January 1957 to November 24, 1957, samples were obtained from five females from each school fished. From November 24, 1957, to the end of the survey in the Marquesas, 10 were obtained from each school, five from females and five from males. When fewer than 10 fish were caught, samples were obtained from the entire catch. In Hawaii all of the skipjack sampling was carried out from commercial fishing vessels. During the initial phases of the study, 20 samples were taken from each school whenever possible. Later the number was reduced to 10. No attempt was made to obtain equal representation of the sexes. The Marquesan samples were obtained within a radius of 250 miles from the island of Nuku Hiva, while those from Hawaii were obtained within a radius of 150 miles from the island of Oahu.

Comparisons between infestation rates were made by chi-square tests (Snedecor, 1956). The hypothesis of no difference was rejected if the probability of chi-square was less than 0.05.

IDENTIFICATION OF TREMATODE

Representatives of the genus *Hirudinella*, digenetic trematodes belonging to the family Hemiuridae, have been reported from the stomachs of a number of scombriform fishes. Depending upon the state of contraction, they may be less than 2 and greater than 5 centimeters in length, but most of our preserved specimens were between 2 and 5 centimeters. Their life cycle is presently unknown.

The genus has been studied in detail by Nigrelli and Stunkard (1947). They ascribed the giant trematodes from the wahoo, *Acanthocybium solanderi* (Cuvier and Valencien-

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nes), to *H. ventricosa* (Pallas). Although uncertainty was expressed about the identification of the giant trematodes found in other hosts, they considered them to belong to a single species, *H. marina* Garcin, on the basis of various morphological differences from *H. ventricosa.* The hosts of *H. marina* included the following species of scombriform fishes: *Parathunnus atlanticus* (Lesson), *Katsuwonus pelamis* (Linnaeus), *Euthynnus alletteratus* (Rafinesque), *Neothunnus macropterus* (Temminck and Schlegel), *Makaira mitsukurii* (Jordan and Snyder), *Scomberomorus maculatus* (Mitchill), and *Thunnus thynnus* (Linnaeus).

SINGLE AND MULTIPLE OCCURRENCES

H. marina was found in 311 of the 1,130 skipjack tuna stomachs examined. One trematode per stomach was most common. Only eight of the stomachs had more than two trematodes. The highest number found in a single stomach was four (Table 1). Although Iversen and Yoshida (1957) found as many as 17 *H. ventricosa* in a single wahoo stomach, they reported two *H. ventricosa* per stomach as the most common occurrence.

Trematodes occurred more often in skipjack stomachs collected in Hawaiian waters than in those collected in Marquesan waters (Table 1). Chi-square tests showed the differences between the two areas to be significant in the total number of stomachs infested ($\chi^2 = 26.434$; $p < 0.0001$) and also in the number of stomachs containing one trematode ($\chi^2 = 20.412$; $p < 0.0001$), but nonsignificant in the number of stomachs containing more than one.

The percentages of trematode occurrences, 20.6 percent for Marquesan skipjack and 34.3 percent for Hawaiian skipjack, are similar to those for other tunas caught in central Pacific waters. King and Ikehara (1956: page 66) found 32 percent of 166 bigeye (*Parathunnus sibi*) and 26 percent of 439 yellowfin (*Neothunnus macropterus*) with the trematodes in their stomachs. These trematodes were stated very likely to be *H. marina* by Iversen and Hoven (1958). These rates contrast sharply with the incidence of *H. ventricosa* in 98.2 percent of 220 wahoo caught in the area of the Line Islands (Iversen and Yoshida, 1957).

INCIDENCE BY SEX

The infestation rates for males and females from the two areas showed a significant difference between sexes for Marquesan skipjack tuna ($\chi^2 = 17.765$; $p < 0.0001$), but not for Hawaiian. Examination of the data indicated that this difference was probably due to the high incidence in the exclusively female samples obtained in January, February, and March of 1957. When the comparison was based on data only from those months in which both sexes were represented, the difference between sexes within the Marquesas (15.0 percent for females and 10.8 percent for males, Table 2) was not significant. Comparison within months of the infestation rates between sexes showed no significant differences in the months during which both sexes had been sampled for either Marquesan or Hawaiian skipjack.

Separation of the data into length groups from schools which had both sexes sampled (Table 2) revealed significant differences between sexes for only the 40.0–49.9-centimeter Marquesan skipjack ($\chi^2 = 4.472$; $p < 0.05$). The rest of the length groups for the Marquesan area and all for the Hawaiian area showed no significant difference between sexes.

Comparison of the incidence of trematodes in the same sex from the two areas showed significant differences. The 21 out of 195 for the Marquesan male skipjack was significantly less than the 91 out of 280 for the Hawaiian male skipjack ($\chi^2 = 29.761$; $p < 0.0001$), as was the 94 out of 363 for Marquesan female skipjack from the 92 out of 261 for Hawaiian female skipjack ($\chi^2 = 6.366$; $p < 0.02$).

While making the above comparisons, the

TABLE 1.—*Summary of single and multiple occurrences of giant trematodes in stomachs of skipjack tuna from the Marquesas and Hawaii*

[Percentage occurrences in parentheses]

Area	Number of stomachs examined	Number of stomachs containing:					Total number of stomachs containing trematodes
		0 Trematode	1 Trematode	2 Trematodes	3 Trematodes	4 Trematodes	
Marquesas	558	443 (79.4)	75 (13.4)	37 (6.6)	3 (0.5)	0 (0)	115 (20.6)
Hawaii	572	376 (65.7)	137 (24.0)	54 (9.4)	4 (0.7)	1 (0.2)	196 (34.3)

TABLE 2.—*Giant trematode incidences in stomachs of male and female skipjack tuna of various lengths from the Marquesas and Hawaii*

Item	Length group (centimeters)						Total
	30.0–39.9	40.0–49.9	50.0–59.9	60.0–69.9	70.0–79.9	80.0–89.9	
			Marquesas[1]				
Male							
Number of stomachs	—	104	55	5	29	2	195
Number with trematodes	—	5	10	1	4	1	21
Percentage infestation	—	4.8	18.2	20.0	13.8	50.0	10.8
Female							
Number of stomachs	1	124	40	6	27	2	200
Number with trematodes	0	16	9	1	4	0	30
Percentage infestation	0	12.9	22.5	16.7	14.8	0.0	15.0
Both sexes							
Number of stomachs	1	228	95	11	56	4	395
Number with trematodes	0	21	19	2	8	1	51
Percentage infestation	0	9.2	20.0	18.2	14.3	25.0	12.9
			Hawaii[2]				
Male							
Number of stomachs	1	29	31	16	159	18	254
Number with trematodes	0	4	14	9	49	6	82
Percentage infestation	0	13.8	45.2	56.2	30.8	33.3	32.3
Female							
Number of stomachs	—	25	32	20	155	5	237
Number with trematodes	—	5	13	10	56	2	86
Percentage infestation	—	20.0	40.6	50.0	36.1	40.0	36.3
Both sexes							
Number of stomachs	1	54	63	36	314	23	491
Number with trematodes	0	9	27	19	105	8	168
Percentage infestation	0	16.7	42.9	52.8	33.4	34.8	34.2

[1] Data from schools which did not have both sexes sampled are not included.
[2] Length data for 60 samples were not available. Ten of these plus 21 others had no sex data available.

magnitude of the between-year difference, particularly of females in the Marquesas, was noticed. Since the data from the two areas did not cover the same period of time, it was necessary to determine whether differences existed between years within sexes of the same area. For the Marquesas the incidence of trematodes in females during 1957 was significantly greater than that in the females during 1958 ($\chi^2 = 35.852$; $p < 0.0001$). Comparable data were unavailable for males. For Hawaii no yearly differences were found for females, but for males a significant difference was found between 1956 and 1957 ($\chi^2 = 7.907$; $p < 0.01$).

INCIDENCE BY SIZE

Since there was only one length group which showed a significant difference between sexes (the 40.0–49.9-centimeter group for the Marquesas), the data for the two sexes were combined for comparisons between length groups. No significant difference was observed between sizes in the Marquesas, but a significant difference was observed for Hawaii ($\chi^2 = 15.060$; $p < 0.005$). As seen in the data tabulated in the lines labeled "Both sexes" in Table 2, there was a higher incidence in the Hawaiian skipjack than in Marquesan skipjack for each length group. Significant differences between the same length groups from the two areas were observed for the 50.0–59.9-($\chi^2 = 9.652$; $p < 0.003$), 60.0–69.9-($\chi^2 = 4.215$; $p < 0.05$), and 70.0–79.9-($\chi^2 = 8.250$; $p < 0.005$) centimeter groups.

INCIDENCE BY SEASON AND YEAR

To make seasonal comparisons of trematode incidences, the data were divided into "season" and "off-season" (Table 3). The season months for Hawaii include May, June, July, August, and September, since the highest catch from the commercial fishery for Hawaiian skipjack occurs during these months (Yamashita, 1958). Similar seasonal catch data are not available for the Marquesan region, because a commercial fishery does not exist there. Wilson and Austin (1957), however, have reported that more than three times as many skipjack schools were sighted in the Marquesas during the southern hemisphere summer as during the southern hemisphere winter. Data for the months of November, December, January, February, and March were combined and designated as the "season" period for the Marquesan region. The remaining months were lumped together as the "off-season" for each of the areas.

No significant seasonal differences were found within the same years and same areas. When the 1957 season was compared with the 1958 season (Table 3) for the Marquesas, however, a significant difference was observed

TABLE 3.—*Seasonal and yearly variations of giant trematode incidences in stomachs of skipjack tuna from the Marquesas and Hawaii*

Item	Year			Total
	1956	1957	1958	
Marquesas				
Season				
Number of stomachs	—	128[1]	283	411
Number with trematodes	—	57	38	95
Percentage infestation	—	44.5	13.4	23.1
Off-season				
Number of stomachs	—	15[1]	132	147
Number with trematodes	—	4	16	20
Percentage infestation	—	26.7	12.1	13.6
Hawaii				
Season				
Number of stomachs	383	129	—	512
Number with trematodes	117	57	—	174
Percentage infestation	30.5	44.2	—	34.0
Off-season				
Number of stomachs	40	20	—	60
Number with trematodes	16	6	—	22
Percentage infestation	40.0	30.0	—	36.7

[1] These samples were from female skipjack only.

($\chi^2 = 47.708$; $p < 0.0001$), as was the case for the Hawaiian area when the 1956 season was compared with the 1957 season ($\chi^2 = 7.808$; $p < 0.01$). Differences between the off-seasons of 1957 and 1958 for the Marquesas and of 1956 and 1957 for Hawaii were not significant. For the Marquesas data, it is possible that the difference between seasons may have been influenced by the nonrepresentation of males in the 1957 samples. Accordingly, the 1958 data for male skipjack were eliminated. The season difference for 1957 and 1958 was still significant ($\chi^2 = 26.895$; $p < 0.0001$). The off-season difference was not. Comparison of season ($\chi^2 = 12.598$; $p < 0.0005$) and off-season ($\chi^2 = 13.923$; $p < 0.0003$) totals showed that the trematode incidences in Hawaiian skipjack were significantly higher than in Marquesan skipjack. When the data were rearranged and examined for differences between years within the same length group and within the same area, significant differences were found in three length groups from the Marquesas: 40.0–49.9-centimeter ($\chi^2 = 13.494$; $p < 0.0003$), 50.0–59.9-centimeter ($\chi^2 = 4.334$; $p < 0.05$), and 60.0–69.9-centimeter ($\chi^2 = 9.892$; $p < 0.003$). For the area of Hawaii, only one length group, 60.0–69.9-centimeter ($\chi^2 = 5.730$; $p < 0.03$), showed a significant yearly difference.

The results to this point led to a final comparison, a between-area, within-year comparison, for which only the 1957 data could be used. The difference was not significant.

DISCUSSION AND CONCLUSION

The contrast in the trematode incidences between Hawaiian skipjack tuna and Marquesan skipjack tuna led to the hypothesis that this difference was due to area. Significant differences revealed by the following comparisons supported the hypothesis: males and females from the Marquesas versus those from Hawaii, length groups from the Marquesas versus corresponding length groups from Hawaii (for the 50-, 60-, and 70-centimeter groups), and seasons and off-seasons in the Marquesas versus those in Hawaii.

Within area comparisons of the following categories, however, also yielded significant differences: females of different years in the Marquesas, males of different years in Hawaii, seasons of different years of both areas, length groups in Hawaii, and within certain length groups of different years (the 40-, 50-, 60-centimeter groups of the Marquesas and the 60-centimeter group of Hawaii). All of the differences within area are associated with time and size. Since size itself is associated with time, it appears that a major source of variation may be attributed to time. That time was a more important factor in the observed differences is supported by the data of 1957, the only year common to both areas. The difference between the two areas was not significant for that year. Regrettably, the data from the two areas, collected incidentally to other studies, do not cover the same years. Thus, they do not permit a measure of the time variable in those comparisons which show an inter-area difference.

In conclusion, the difference observed between the incidences of *Hirudinella marina* in skipjack tuna from Hawaii and from the Marquesas seems to be associated with time rather than area. Whether or not a real difference does exist between these areas could not be determined from the available data.

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The Identification of Larval Yellow Perch, *Perca flavescens* and Walleye, *Stizostedion vitreum*

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BIOLOGISTS have long recognized the necessity of correctly identifying the larvae and very young of fishes when they investigate the life history, distribution, spawning success, and even the systematics of a species. In the past, authors have used such characters as location and concentration of pigment (Pritchard, 1930; Fish, 1932; Balinsky, 1948; Winn and Miller, 1954; Mansueti, 1956), myomere counts (Leim, 1924; Fish, 1932), and pre- and postanal measurements (Winn and Miller, 1954) as a means of identifying larval fishes.

The purpose of this study was to present data that could be used to distinguish some of the larval fishes of the Great Lakes; in particular, the walleye, *Stizostedion vitreum* (Mitchill) and the yellow perch, *Perca flavescens* (Mitchill). It was found that the best way to distinguish walleye from yellow perch larvae was the postanal myomere count, the length of the yolk sac, the length of the intestine, the snout-to-anus and anus-to-caudal measurements, and the location of the lower jaw articulation. Pigmentation and chromatophore development, although of some value are quite variable, showing rather conspicuous differences among larvae collected from different bodies of water.

Much of the initial work was done while I was employed by the United States Department of the Interior, Bur. of Commercial Fisheries' Great Lakes Laboratory at Ann Arbor, Michigan during the summers of 1958 and 1959. I wish to thank Mr. John Parsons, Leonard Joeris, Ernest Korvelis, and Dr. Alfred M. Beeton of the Great Lakes Laboratory for their efforts in securing specimens.

MATERIALS AND METHODS

Approximately 1186 larval and very young yellow perch with a range of 5.4 to 43.3 mm.

in total length (T.L.) and 235 larval and very young walleye 7.4 to 33.5 mm. T. L., were used in the study.

Most of the specimens were collected in the Great Lakes with one-quarter and one-half meter plankton nets of various mesh sizes. These were attached to trawls in conjunction with investigations of the U. S. Fish and Wildlife research vessel *Cisco* in Lake Erie during 1957 and 1958 and the *Musky* in Lake Erie during 1957–59. Larvae were also collected by small trawls towed from outboard motor boats in northern Green Bay, Lake Michigan, and in Sandusky Bay and other areas of western Lake Erie. A few of the walleye larvae came from hatchery stock at Put-in-Bay, Ohio.

The larval fishes were preserved in 10 percent formalin and many were studied in this preservative under a compound binocular microscope. Others were partially cleared in 3 percent KOH so that the internal anatomy was more clearly visible. Samples of various stages were cleared in 3 percent KOH, stained in alizarin red, and preserved in glycerine as prescribed by Evans (1948), in order to determine early centers of ossification.

Measurements were taken with an ocular micrometer, or with calipers under the low-power of a binocular dissecting microscope. The total length is the distance from the anterior tip of the snout to the posterior tip of the caudal finfold or caudal fin. The snout-to-anus measurement is the distance from the anterior tip of the snout to the anus. The anus-to-caudal measurement is the distance from the anus to the posterior tip of the caudal finfold or caudal fin. The intestine length is the distance from the posterior margin of the yolk sac to the anus in the prolarvae, or from the posterior margin of the stomach to the anus in the postlarvae. The length of the yolk sac is the longest anterior-posterior dimension. The preanal myomeres are all those from the nape to the posterior end of the anus. The postanal myomeres are all the remaining myomeres from the anus to the caudal fin.

Following the work of Hubbs (1943), and Winn and Miller (1954), an attempt was made to divide the larvae into two categories: the prolarval stage in which the yolk sac was present, and postlarval stage after the absorption of the yolk sac, until the juvenile characters were attained. Since growth and development proceed so rapidly in these two species it was necessary to subdivide the larvae into one mm. length intervals.

Prolarva

Larval yellow perch (Fig. 1) in this stage of development are from 5.5 to about 7.0 mm. T.L., whereas the walleye prolarvae (Fig. 4) are from 7.4 (Ryder, 1887:519, gives 5.8 mm.) to about 9.6 mm. In both species the notochord is straight and the finfolds are complete. In the yellow perch the dorsal finfold commences at the base of the first myomere and is almost straight to the caudal; in the walleye it commences about the third to the sixth myomere and there is a slight rise posterior to the vent. The ventral finfold of the two species, commences along the posterior margin of the yolk sac, breaks at the anus and then continues to the caudal fin. It is widest just posterior to the anus. Both species have pectoral fin buds but not the pelvics, and such cartilaginous elements as the dentaries, branchial arches, semicircular canals, and cleithra are distinguishable.

The yolk sac of the yellow perch is an ovate structure about 1.1 to 2.3 mm. in length (Table 1) and 0.4 to 0.8 mm. in width, and it becomes smaller as development proceeds so that it is no longer feasible to measure after the larvae are about 6.8 mm. The yolk sac of the walleye is more elongated, about 2.1 to 2.6 mm. in length and about 0.8 to 1.3 mm. in width (Table 1). It too becomes smaller as development proceeds so that it becomes impractical to measure after the larvae have reached a length of 9.4 mm. Both have a clear, round oil globule at the anterior end of the yolk sac. The intestine, from the posterior margin of the yolk sac to the anus, is straight and from 0.5 to 1.1 mm. in length (Table 1) in the yellow perch. It is shorter in the walleye, from 0.3 to 0.7 mm. in length (Table 1) and bends abruptly downward to the anus. The anus-to-caudal measurement of the yellow perch is slightly less than the snout-to-anus measurement whereas in the walleye prolarvae the anus-to-caudal measurement is greater (about 10 percent) than the snout-to-anus measurement (Table 1). The yellow perch has from 17 to 21 (18) preanal and from 17 to 20 (18) postanal myomeres whereas the walleye has 16 to 20 (18) preanal and 25 to 28 (26) postanal myomeres.

Pigmentation is rather sparse in the prolarval yellow perch (Fish, 1932:362). A pair of large, stellate chromatophores appear over the oil globule and from six to ten over the remainder of the yolk sac. One, two, or three large chromatophores are found near the anus and a few smaller ones occur along the

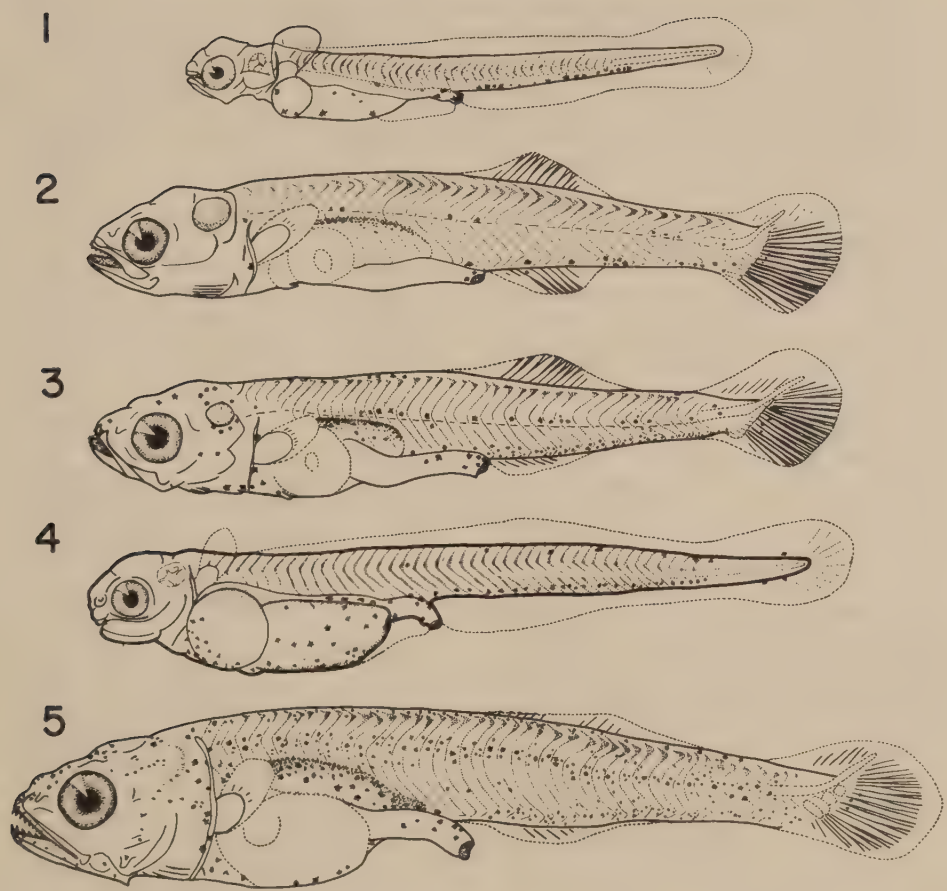

Fig. 1. *Perca flavescens* (Mitchill) Prolarva. Total length = 5.8 mm. Lake Erie. May 14, 1959.
Fig. 2. *Perca flavescens* (Mitchill) Postlarva. Total length = 13.0 mm. Lake Erie. June 6, 1959.
Fig. 3. *Perca flavescens* (Mitchill) Postlarva. Total length = 13.0 mm. Lake Michigan. June 2, 1959.
Fig. 4. *Stizostedion vitreum* (Mitchill) Prolarva. Total length = 8.0 mm. Lake Erie. May 14, 1959.
Fig. 5. *Stizostedion vitreum* (Mitchill) Postlarva. Total length = 14.8 mm. Lake Michigan. June 2, 1959.

dorsal margin of the intestine. A ventral line of 15 to 20 small chromatophores may be seen commencing at the anus and ending near the caudal fin.

Pigmentation in the walleye prolarvae is more profuse. The yolk sac has many small, stellate chromatophores scattered over its lateral and ventral surfaces. From two to four chromatophores are usually present on the intestine between the anus and the yolk sac and occasionally one or two are visible on the lateral margin of the lower jaw. The ventral pigment line, beginning at the anus and extending on to the caudal fin is well developed, with one or more chromatophores per body segment. A few small chromatophores are faintly visible in the visceral pigment line, dorsal to the yolk sac and one or two are present along the dorsal pigment line in the region of the caudal fin.

Postlarva

Yellow perch larvae in this stage of development are from 7.0 to 35.0 mm. in T.L. (Figs. 2 and 3) and the walleye larvae are from 9.5 to about 40.0 mm. long (Fig. 4). The finfolds gradually disappear and are practically gone when both species reach a length of 13.0 mm. Ossified rays first appear in the ventral half of the caudal fin (between 8.0 and 9.0 mm. T.L.) in the yellow perch and at 10.5 mm. in the walleye (Table

TABLE 1. PRINCIPAL CHARACTERS USED TO DISTINGUISH EARLY DEVELOPMENTAL STAGES OF THE YELLOW PERCH FROM THE WALLEYE

Character	Yellow perch, *Perca flavescens*		Walleye, *Stizostedion vitreum*	
	Measurements or Numbers	Number of Specimens	Measurements or Numbers	Number of Specimens
Prolarva				
Total length	5.5–7.0 mm.	42	7.4–9.6 mm.	45
Yolk Sac				
Length	1.1–2.3 mm.	24	2.1–2.6 mm.	21
Width	0.4–0.8 mm.	24	0.8–1.3 mm.	21
Intestine				
Length	0.5–1.1 mm.	35	0.3–0.7 mm.	30
Snout-to-anus	3.0–3.8 mm.	24	3.5–4.5 mm.	26
Anus-to-caudal	2.6–3.5 mm.	24	3.6–5.5 mm.	26
Myomere number				
Preanal	17–21 (18)	42	16–20 (18)	44
Postanal	17–20 (18)	42	25–28 (26)	44
Pigmentation	Ventral pigment line of 15 to 20 small chromatophores. Few on yolk sac.		Ventral pigment line well developed. Numerous chromatophores on ventral surface of yolk sac.	
Postlarva				
Total length	7.0–35.0 mm.	78	9.5–32 mm.	42
Myomere number				
Preanal	17–22 (19)	78	16–24 (19)	42
Postanal	16–21 (19)	78	22–29 (26)	42
Articulation of lower jaw	Below the orbit.		Below posterior margin of orbit.	
Teeth	Small, non-canine.		Larger, with some canine-like.	
Pigmentation	Dorsal, lateral, visceral pigment lines poorly developed. Few chromatophores on top of head, cheeks, and jaws.		Dorsal, lateral, visceral, and ventral pigment lines well developed. Chromatophores abundant on top of head, cheeks, and jaws.	

TABLE 2. TOTAL LENGTH AT WHICH CERTAIN MERISTIC CHARACTERS COMMENCE TO OSSIFY

Character	*Perca flavescens*			*Stizostedion vitreum*		
	Total length Intervals (mm.)	Number of Elements	Number of Specimens	Total length Intervals (mm.)	Number of Elements	Number of Specimens
Caudal fin rays	8.0–8.9	0 to 10	8	10.0–10.9	0 to 11	12
Branchiostegal rays	9.0–9.9	0 to 4	17	10.0–10.9	0 to 4	12
Vertebrae	9.0–9.9	0 to 27	17	12.0–12.9	0 to 23	5
Dorsal fin rays	12.0–12.9	0 to 6	10	13.0–13.9	0 to 11	7
Anal fin rays	12.0–12.9	0 to 3	10	12.0–12.9	0 to 3	5
Pectoral fin rays	13.0–13.9	0 to 5	7	15.0–15.9	0 to 7	3
Dorsal spines	13.0–13.9	0 to 9	7	15.0–15.9	5 to 13	3
Anal spines	13.0–13.9	0 to 2	7	15.0–15.9	1 to 2	3
Pelvic fin rays	15.0–15.9	0 to 4	3	16.0–16.9	0 to 4	2

2). Ossified rays appear in the dorsal and anal fins at about the same time, at 12.0 to 13.0 mm. T.L. in the yellow perch and at 13.0 to 14.0 mm. T.L. in the walleye, although in one specimen three anal fin rays were partially ossified in a larva 12.6 mm. long (Table 2). Pectoral fin rays, dorsal, and anal spines are beginning to ossify when the

TABLE 3. TOTAL LENGTH AT WHICH CERTAIN BONES COMMENCE TO OSSIFY

Bones	*Perca flavescens*			*Stizostedion vitreum*		
	Total Length Intervals (mm.)	Number Examined	Number with Ossification	Total Length Intervals (mm.)	Number Examined	Number with Ossification
Cleithrum	7.0–7.9	16	3	9.0–9.9	9	4
Dentary	7.0–7.9	16	2	9.0–9.9	9	3
Premaxilla	7.0–7.9	16	2	9.0–9.9	9	6
Dentary teeth	7.0–7.9	16	2	9.0–9.9	9	1
Ceratobranchials	7.0–7.9	16	2	9.0–9.9	9	1
Maxilla	8.0–8.9	8	6	10.0–10.9	12	6
Premaxillary teeth	8.0–8.9	8	5	10.0–10.9	12	6
Branchial arches	8.0–8.9	8	2	10.0–10.9	12	10
Quadrate	9.0–9.9	17	1	10.0–10.9	12	2
Frontal	10.0–10.9	19	3	12.0–12.9	5	2
Preopercle	10.0–10.9	19	1	12.0–12.9	5	4
Opercle	10.0–10.9	19	3	12.0–12.9	5	5

larval yellow perch are between 13.0 and 14.0 mm. T.L. whereas these elements commence to ossify between 15.0 and 16.0 mm. T.L. in the walleye larvae. The pelvic fin rays are the last to ossify in both species, at 15.0 to 16.0 mm. T.L. in the yellow perch and at 16.0 to 17.0 mm. in the walleye.

The first bones to show any evidence of ossification (at 7.4 mm. in the yellow perch and at 9.5 mm. in the walleye) are the cleithra, dentaries, premaxillae, and ceratobranchials (Table 3). At 8.3 mm., teeth are visible on the premaxillae and ossification is commencing in the maxillae and branchial arches of the yellow perch. This does not occur in the walleye until they have reached a length of 10.5 mm. However, the qradrates and branchiostegal rays are also ossifying at this stage (Tables 2 and 3). This stage compares favorably with the largest specimen (Fig. 64) illustrated by Reighard (1888). In the yellow perch, these bones (quadrates and branchiostegal rays) as well as the vertebrae commence to ossify when the larvae are between 9.0 and 10.0 mm. T.L. At 10.0 to 11.0 mm. in length the deposition of bone is occurring in the opercle, preopercle, and frontal bones of the yellow perch. The articulation of the partially ossified lower jaw is now clearly visible, it being located below the orbit. The opercle, preopercle, frontal, and vertebrae commence to ossify in the walleye at 12.0 to 13.0 mm. T.L. The articulation of the lower jaw is located below or behind the posterior margin of the orbit (Fig. 5). The deposition of bone is continuous and rapid from this time onward and at 18.0 mm. all bones are in various stages of ossification. In yellow perch larvae, scales first appeared at size intervals of 21.0 to 22.0 mm. In the largest walleye specimen available (33.5 mm.) scales had not yet appeared.

The intestine of the yellow perch is rather elongate, being almost twice the length of the lower jaw. In the walleye, the intestine is somewhat coiled near the stomach but posterior to the stomach it is almost straight to the anus, measuring about 15 percent of the total length of the fish and approximately equal to the length of the lower jaw.

Seventeen to 22 (19) preanal and 16 to 21 (19) postanal myomeres are present in the postlarval yellow perch, whereas 16 to 24 (19) preanal and from 22 to 29 (26) postanal myomeres are present in the walleye. Thus the myomere count is closely correlated with the number of vertebrae as tabulated by Bailey and Gosline (1955:10).

Pigmentation is more profuse in the postlarval walleye and becomes increasingly so with size and age (Reighard, 1888; Fish, 1932). The dorsal pigment line, commencing at the head and continuing to or near the caudal fin, is usually double. One row lies dorsal to the notochord with from one to four chromatophores per myomere while the second row is found along the mid-dorsal region of the body, with one or two chromatophores per segment. The lateral pigment line is well developed in all postlarval stages. These lateral chromatophores, from one to four per myomere, are located in the dermis

at a level with and just below the notochord. The visceral pigment line is very conspicuous with numerous chromatophores located dorsal to and around the air bladder. Chromatophores are also plentiful dorsal to the intestine but decrease in number near the anus, with from two to six present near the vent. The ventral pigment line runs from the anus onto the caudal fin, with one, two, or three chromatophores per segment. Large stellate chromatophores are abundant on top of the head, from the tip of the snout to the nape, on the cheeks, at the base of the pectoral fin and in the region of the heart. In addition, the sides and tips of both jaws are fairly well pigmented.

The concentration of pigment in the postlarval yellow perch gradually increases with age, although less so than in the young walleye. A similar observation was reported by Fish (1932). Pigment characters are difficult to describe in the postlarvae because those collected from Lake Michigan are much darker than those of equal size collected from Lake Erie. There is little difference in chromatophore development in the prolarvae from these two lakes but at size ranges from 12.0 to 18.0 mm. the Lake Michigan postlarvae (Fig. 3) are readily separable from the Lake Erie postlarvae (Fig. 2).

In specimens from Lake Erie, the dorsal pigment line is usually obsolete whereas the Lake Michigan specimens have eight or more widely scattered chromatophores. The lateral pigment line is incompletely developed in larvae from both lakes, although in the Lake Michigan specimens chromatophores are more numerous in the area from the anus to the caudal fin. The visceral pigmentation, dorsal to the air bladder, is very concentrated in specimens from the two lakes, but along the entire length of the intestine there are only one or two chromatophores in the Lake Erie larvae whereas those from Lake Michigan have from two to seven. The ventral pigment line, from the anus to the caudal fin, is well developed in both, but a greater concentration appears on the Lake Michigan specimens, especially on the caudal fin. Six to eight chromatophores are found in the region of the heart in larvae collected from Lake Michigan; those from Lake Erie have only one or two. Chromatophores are more plentiful on the top of the head, on the cheeks, at the tip of the lower jaw and along the pectoral girdle in larvae from Lake Michigan.

This study indicates that pigment characteristics cannot be used to define the postlarvae of the yellow perch with any degree of accuracy and that the larvae of this species differ markedly in the degree of chromatophore development.

Summary

Prolarvae and postlarvae of the yellow perch, *Perca flavescens*, and of the walleye, *Stizostedion vitreum*, can be separated by morphometric and meristic characters, and to a lesser extent by differences in pigmentation. The average number of postanal myomeres in all larvae of yellow perch is about seven less than that found in the walleye at similar stages. The average size of the prolarval yellow perch (5.5–7.0 mm. T.L.) is significantly less than that of the walleye (7.4–9.6 mm. T.L.). There is a similar reduction in the size of the yolk sac in the former species when it is compared with the latter. Other differences include the articulation of the lower jaw which is located below the orbit, the character of the teeth, and the longer intestine in the yellow perch, whereas the articulation of the lower jaw is located below the posterior margin of the orbit, some teeth are canine-like, and the intestine is short in the larval walleye.

Chromatophores are more numerous in all larval stages of the walleye as compared with the yellow perch. They are most distinctive on the yolk sac and on the sides and tips of both upper and lower jaw.

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EFFECTS OF THE FLATWORM STYLOCHUS ELLIPTICUS (GIRARD) ON OYSTER SPAT IN TWO SALT WATER PONDS IN MASSACHUSETTS

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ABSTRACT

During the summer of 1957 the larvae and juveniles of the flatworm Stylochus ellipticus occurred in great abundance in two salt water ponds on Martha's Vineyard Island. Setting rates of flatworms were as high as one per shell per day. Data over a period of three years indicate that such larvae and post-larvae occurred in these ponds only when salinities were below 20°/oo. Mortality of newly set oysters due to depredation by these flatworms was severe, approaching 100% in some samples. Dipping infected oyster spat in a concentrated salt solution proved an effective method of ridding the set of flatworms, but this is an effective remedy only if the treated spat are protected from reinfestation. Because of the widespread distribution of S. ellipticus in many oyster-growing regions in New England and elsewhere the need for a more effective control of its predation on oyster spat is obvious.

The U. S. Fish and Wildlife Service Marine Biological Laboratory at Milford, Connecticut, in cooperation with the Oyster Institute of North America, is engaged in a study designed to develop the principles of shellfish culture in salt water ponds. Two of the ponds under study, West Tisbury Great Pond and Oyster Pond on Martha's Vineyard Island, Massachusetts, are periodically open to the sea and contain populations of soft clams and oysters of economic importance. These ponds are well suited for oyster seed production since they are remarkably free of such oyster enemies as drills, starfish and sponges. However, observations during 3 years of study indicate that the flatworm Stylochus ellipticus is an important predator on oyster spat in these ponds and that the future utilization of such ponds for production of seed oysters may depend on effective control of this pest.

The potential of some polyclad flatworms as oyster enemies has long been known and certain aspects of the biology and predatory nature of related species have been published by Pearse and Wharton (1938), Dawson (1953), and Woelke (1957). Hopkins (1955) ascribed some oyster mortality to Stylochus and Menzel and Hopkins (1956) included Stylochus ellipticus in their list of predators on Louisiana oysters. Loosanoff

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Table 1. Occurrence of larval and post-larval flatworms in Tisbury Pond, 1957.

Date	In Plankton	Salinity o/oo	On biweekly cultch samples #/20 shell faces
20 June	no tow	18	53
21	a few	18	no sample
24	a few	17	24
26	present	17	57
28	present	14-18	no sample
1 July	present	16-17	22
3	present	16	no sample
4	no tow	16.5	4
5	present	16.5	no sample
8	many	15.5-16.5	18
10	present	13	12
12	present	16.5	no sample
15	present	16.5-17.5	6
17	present	15.5-16.5	2
18 Tisbury Pond Opened			
19	present	10.5-13.5	no sample
22	no tow	11.0-11.5	22
25 July - 18 August	absent	21-28	absent
18 August Pond closed		24	
30 September	1 indiv.	15	

(1956) was the first to publish an account of predation on oyster spat by Stylochus ellipticus in the laboratory.

The present paper is a record of observations on the numbers of Stylochus and their predation on oyster set, during 1956, 1957, and 1958 in the two ponds on Martha's Vineyard. During the summer of 1956 very few S. ellipticus, either adults or recently set individuals, were seen. Again in 1958 the population was very sparse. In 1957, however, large numbers of larvae, recently set individuals and adults were observed.

The first indication that this was to be an unusually large year class was the discovery on June 20, 1957 of large numbers of what appeared to be recently set flatworms on Tisbury cultch examined for oyster spat. Continued observations on the development of these animals confirmed their identity. Plankton samples were being taken three times a week with a #20 silk net. On June 21 large numbers of what were assumed to be Stylochus larvae or post-larval stages were noted in the plankton of Tisbury Pond. These forms appeared as miniature flatworms, oval in shape, and measured about 82 x 71 micra. During the first week of July such numbers occurred that they constituted a major component of the zooplankton. Flatworm larvae were also found in the plankton of Oyster Pond, but in smaller numbers. In Tisbury Pond, flatworm set were found in considerable numbers until July 18 when this pond was opened to the sea. Some flatworm larvae were found in Tisbury plankton samples until July 22 but only occasional specimens were found on the biweekly set bags after the pond was opened.

Data for three stations in Tisbury Pond were similar with respect to dates of occurrence of the larvae and approximate numbers of flatworm set per shell. Values for one of the sampling stations are presented in Table 1. The disappearance of flatworm larvae and cessation of flatworm setting just after the pond opening was striking. While it is possible that this would have occurred regardless of whether or not the pond was opened, it is more likely that the disappearance was due to large numbers of larvae being swept out of the pond at the initial opening, for at least one quarter of the pond water was estimated to have escaped within 24 hours of the opening, and additional losses of plankton and pond water occurred with each tidal cycle. Oyster Pond, which was closed most of the summer, continued to show a few flatworms in the plankton but none were found on cultch until July 29 when pond salinity had dropped to 20 o/oo. A few flatworms continued to set during August as salinity continued to fall.

Whether the rapid change in salinity which followed the opening of Tisbury Pond was detrimental to the young flatworms can only be conjectured at this point. Available data from 3 years' observation indicate that planktonic and recently set flatworms occurred in these ponds only when salinities were below 20 o/oo. Menzel and Hopkins (1954) found adult Stylochus ellipticus in abundance only in waters of "relatively low salinity." In several cases in the literature other

species of flatworms were found associated with high rather than low salinities (Dawson 1953, Pearse and Wharton 1938). Apparently each species has its own requirements which need not be similar to those of other members of the same or a related genus. Some adaptability to salinity is to be expected. Woelke (1957) showed that despite a preference for 28 o/oo by Pseudostylochus ostreophagus, that species could tolerate 10 o/oo for as long as a week and even lower salinities for a shorter time.

Predation by Stylochus on oyster set became apparent when on August 7 some cultch bags from Tisbury Pond were examined and in half an hour several hundred flatworms measuring form 1/4 to 1/2 inch in length were found. In some cases as many as 15 worms were found on the two sides of a single shell. Dead oyster spat were common, but at this time there were still some live spat. A number of times flatworms were observed entering live oyster spat up to 1/2 inch in greatest diameter. When the top valves were lifted from recently dead spat, 1-3 flatworms usually were found, occasionally one of them in the act of eating the young oyster. In one instance a small recently set flatworm was observed closely appressed to a two-day-old oyster. The flatworm was slightly smaller than the spat.

To estimate mortality due to flatworms and other causes, samples of broadcast cultch were secured on August 13. These samples yielded 590 dead spat, 33 live spat and 8 flatworms. Only those spat were counted which had grown large enough to leave a scar or be seen with the unaided eye. This meant that a mortality of at least 95% had occurred since setting. There are no drills, and no starfish in either pond. There was no evidence of crab damage and no reason to suspect epidemic disease. Silting was responsible for some of the mortality, for portions of the cultch with spat scars showed blackening from a mud coating over the dead spat. In contrast to the mortality on broadcast shell, a sample of bagged cultch showed 303 dead spat, 179 live spat and 9 flatworms, or a total post-setting mortality of at least 50%. In this case there was virtually no evidence of silting and nearly all mortality could be ascribed to flatworm predation alone.

In Oyster Pond a sample of spat examined in September 1957 and again in October, showed a mortality of 62% for a six-week period. These spat were bagged and had been washed by wave action, so silting was not a factor and there was no evidence whatsoever to indicate causes for mortality except for the presence and behavior of flatworms among the living and dead spat. Survivors had grown well in the interval between examinations.

It is obvious from the above that an outbreak of the nature described would be very serious in a pond culture operation. In an effort to find a method for field control in the summer of 1957, the Milford laboratory began a series of experiments immediately. One suggested method which had been tried experimentally in earlier years

was the use of concentrated salt solution as a dip for infested seed. The method was field tested by immersing bags of cultch with spat into pond water saturated with rock salt. Flatworms curled and after one minute immersion, none recovered. The treatment also killed algae, polychaetes and other organisms associated with the cultch. Eels and toadfish trapped in the bags reacted violently and soon died. After 15-30 minutes draining following a one-minute dip, the bags were divided into two lots. Some bags were placed in a floating raft to keep them off the worm-infested bottom. Although there were no longer large numbers of flatworm larvae in the plankton, a few Stylochus were found on the suspended bags several weeks later. These may have resulted from a few pelagic larvae remaining in the water and setting late, from a few flatworms surviving the dip treatment inside spat boxes or may have been carried to the suspended cultch by water currents. Mortality on the treated bags was arrested but bags replaced on the bottom became reinfested and again began to suffer mortality.

On December 11, 1957 a control sample of untreated bagged cultch was taken from Tisbury Pond. Shells which in August had shown 50% post-setting mortality now yielded 600 scars, 7 live spat and 7 flatworms, a total mortality of at least 99%.

The treatment with salt was effective in killing the flatworms but to be commercially practical in these ponds a method of handling the cultch and seed oysters will have to be developed and methods of preventing reinfestation found.

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Recent Changes in the Walleye Fishery of Northern Green Bay and History of the 1943 Year Class

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Recent Changes in the Walleye Fishery of Northern Green Bay and History of the 1943 Year Class

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ABSTRACT

Production, fishing intensity, and availability of walleyes (*Stizostedion vitreum vitreum*) fluctuated widely in the commercial fishery of northern Green Bay in 1929–57. The catch ranged from 16,000 pounds (8 percent of average for the 1929–53 base period) in 1942 to 1,294,000 pounds (633 percent) in 1950. The index of fishing intensity ranged from 17 (1941) to 400 (1950) and that of abundance from 47 (1929) to 222 (1955). Production and fishing intensity were consistently above average in 1947–57; abundance exceeded the average in 8 of these years. The fishery statistics and records of age and size composition of commercial landings of walleyes in the spring and fall fishing seasons of 1949–58 (scale samples were taken from a total of 1,631 fish) were the basis for a study of recent changes in the walleye fishery with particular reference to the effects of fluctuations in the strength of year classes. The 1943 year class, by a wide margin, exceeded all others in the estimated total number (1,173,000 fish) and weight (3,355,000 pounds) contributed to commercial landings. This year class was a major factor in the sharp rise in production and abundance after 1945 and the all-time record catch of 1950. In contrast, certain other year classes (1945, 1946, 1948) have contributed totals as small as 16,000 to 52,000 pounds. The abundance of the 1950, 1951, and 1952 year classes approached or exceeded that of the 1943 year class at the lesser ages (through the IV group), but these more recent classes disappeared from the fishery so rapidly that their total contributions were relatively low. The indicated increase of mortality in the middle 1950's cannot be attributed to increase in the rate of commercial exploitation. Evidence is offered that the heightened mortality rate resulted from expansion of the sport fishery.

INTRODUCTION

From 1945 to 1957 the walleye (*Stizostedion vitreum vitreum*) fishery of northern Green Bay changed from a small incidental commercial fishery to a major commerical and sport fishery. Hile (1955) has reviewed the recent problems of the fishery and discussed certain controversies which arose. Commercial production of walleyes rose rapidly from 21,000 pounds in 1945 to 1,294,000 pounds in 1950. Commercial fishermen from other parts of the Great Lakes moved to Green Bay to participate in the good fishing, caused extreme competition for good grounds, and created resentment among local fishermen. At the same time, sport-fishing pressure expanded rapidly and extensive resort facilities were built to accommodate the greatly increased numbers of anglers.

Near the height of this expansion various interests sought to restrict the commercial fishery in the hope of preserving the abundant supply of fish. Scale samples taken in the spring of 1949 indicated, however, that the abnormally high abundance of walleyes was caused by a single year class hatched in 1943. Since it was expected that the supply of walleyes would soon decline to a lower level regardless of restrictions on the fishery, most of the proposed restrictions were not adopted. Production and abundance declined drastically in 1951 and 1952, and since the production of the commercial fishery had averaged only 51,000 pounds in 1929–43, it was believed that extremely high abundance probably would not occur again soon. Another peak in abundance was reached in 1955, however, and good fishing continued through 1956.

The purpose of this study is to examine the statistics and age distributions of fish of the commercial fishery for walleyes in Green Bay to obtain information on the contributions of year classes that have passed through the fishery since 1949, especially the 1943 year class. Several people aided in the collection of scale samples. Stanley Lievense of the Michigan Department of Conservation obtained the first scale samples in 1949. Robert Balch, formerly with the Wisconsin Conservation Department, took most of the 1949 and 1950 samples. Leonard S. Joeris and other biologists of the Bureau of Commercial Fisheries took all samples from 1951 through 1958. Several commercial fishermen aided in collection of scales. Ralph Hile offered help in treatment of the data and read the manuscript.

MATERIALS AND METHODS

Scale samples and records of length and weight of walleyes from the commercial fish-

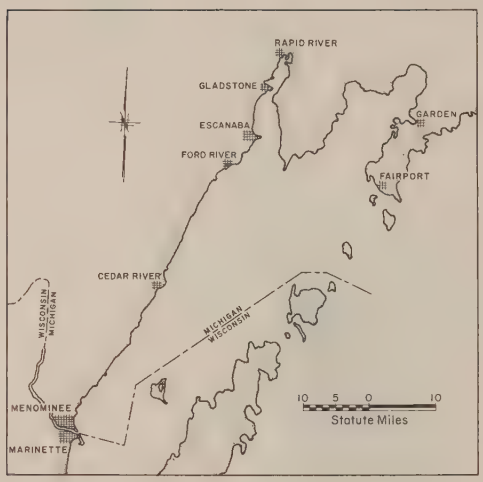

FIGURE 1.—Map of northern Green Bay.

ery were collected by biologists of the States of Wisconsin and Michigan and the U. S. Bureau of Commercial Fisheries. Shortages of personnel and funds prevented thorough coverage of the fishery and left several serious gaps in the data. No coverage of the sport fishery other than general observations was possible. The commercial fishery statistics used are those routinely collected by the State of Michigan and turned over to the Bureau for analysis. Statistical district M-1 encompasses all of the Michigan waters of Green Bay (Figure 1).

Scale samples were taken principally in May and October during the spring and fall peaks of production (Table 1). Spring samples from impounding gear were obtained in all years but one (1952) from 1949 through 1958. Fall samples from these gears were taken in 5 of these 10 years. Three samples were taken from gill nets—September 1949, October 1950, and February 1957. All samples were net-run, but no fish smaller than the legal minimum of 15½ inches, total length, were considered in the present study.

Difficulties in reading the scales were few. Both gelatin mounts and plastic impressions were exceptionally clear. The timing of the collections (spring and fall) eliminated the difficulties of age determination that can be caused by annulus formation, since walleyes grow only in June–September in Green Bay. Throughout this study age refers to the number of annuli. Scales from spring samples were credited with a virtual annulus on the edge of the scale. Although validation of scale reading is not a part of this study, the persistent occurrence of strong and weak year classes in successive years of collection and the presence of some years of exceptionally good and poor growth gave evidence of a high level of accuracy in the reading. Ages were determined for 816 fish from the spring and 472 fish from the fall impounding-gear fisheries, and 343 fish from the gill-net fishery.

TABLE 1.—*Scale collections from legal-sized walleyes in the commercial fishery of northern Green Bay*

Year and season	Impounding nets	Gill nets	Total
1949			
Spring	109	–	109
Fall	–	171	171
1950			
Spring	57	–	57
Fall	86	72	158
1951			
Spring	46	–	46
Fall	–	–	–
1952			
Spring	–	–	–
Fall	222	–	222
1953			
Spring	37	–	37
Fall	–	–	–
1954			
Spring	70	–	70
Fall	33	–	33
1955			
Spring	47	–	47
Fall	57	–	57
1956			
Spring	141	–	141
Fall	–	–	–
1957			
Spring	158	100	258
Fall	74	–	74
1958			
Spring	151	–	151
Fall	–	–	–
Total			
Spring	816	100	916
Fall	472	243	715
Grand total	1,288	343	1,631

Samples from both impounding nets and gill nets were used for estimates of the contributions of age groups and year classes to the commercial production. Samples from gill nets had age distributions that agreed very closely with those taken from impounding nets the same season or were consistent with samples from impounding nets taken in other seasons. No differences could be detected among the various impounding gears. Other gears contributed so little to the total take that even had the age composition of their catches differed from that in impounding and gill nets the estimates based on the catch of major gears still would be valid.

Estimates of the availability of the various age groups in terms of pounds and numbers per unit effort were made from age data for all gears, but statistics on catch per unit effort were for shallow trap nets only. Most of the production from impounding gear came from trap nets during the period of sampling.

The gaps in the sampling schedule (Table 1) made a number of estimates necessary to obtain a continuing sequence of records that could serve as the basis for a coherent account of the fluctuations in the walleye fishery. All estimates are to some degree uncertain, but the range of fluctuation of year-class strength was so great that any errors made were relatively of such minor magnitude that the general conclusions on trends of the fishery are believed to be sound. Rather than interrupt the continuity of later sections with a series of explanations of the assumptions and computational methods, a statement of types of estimates, of procedures followed, and of the basis for the procedures is offered now. References are made to appropriate tables of later sections.

In order to make reasonable estimates of production by year classes from the spring and fall peaks of production, estimates were made of missing age distributions. The estimated age distribution for the spring of 1952 is the same as that of the sample from the fall of the same year except that the III-group was omitted. A comparison of spring and fall samples in other years indicated that, with this omission, the error was small. In no year were III-group fish important in the spring catch.

The age distribution for the fall of 1953 was set up on the assumption that the year-class composition in that season was identical to that in the subsequent spring. Since few age groups were represented in this year, the procedure was believed to be justifiable. The age distribution for the fall of 1956 was computed by averaging the percentage of fish in each year class in the previous and following spring. Since there was no spring sample in 1952, the 1951 fall distribution was computed by averaging the percentages for 1950 and 1952 fall samples in the same manner. Samples taken at several times of the year in 1957 showed that changes in age composition during the year were gradual and progressive in all but age-groups II and III. The averaging of samples of the previous and following years should, therefore, provide a reasonable estimate of age composition. The estimated percentage age compositions (see Table 6 and Figure 3 of a later section) were all consistent with the actual samples.

TABLE 2.—*Average weights of walleyes in spring and fall samples, 1949–57*

Age group	Weight (pounds)	
	Spring	Fall
II	–	1.31
III	1.30	1.46
IV	1.54	2.40
V	1.98	2.98
VI	2.84	3.00
VII	3.11	3.96
VIII	3.13	4.04
IX	4.13	4.37
X	5.69	7.32
XI	6.01	5.86

The weights of age groups employed for the estimation of the numerical and poundage contribution of age groups and year classes to the commercial take were based on the pooled samples (spring and fall separately) of all years' collections. The average weight of fish of the same age and caught in the same season varied somewhat, but without trend, from year to year. Some of this variability may have been caused by annual fluctuations of growth rate, but most of it is believed to result from the small numbers of fish in most samples and the combined effects of sex differences in growth rate and variation of the sex ratio. (Females are much heavier than males of the same age, particularly at the higher ages.) The pooled sample (Table 2), therefore, probably gives a better estimate of the true average weight of an age group in a particular year than does the small sample of the age group taken in that year.

Estimates were made of contributions of the 1943 and 1944 year classes to the fishery in 1946, 1947, and 1948—as early as 3 years before sampling was started (Tables 7 and 8). The tripling of the catch in 1946 over that of 1945 (Table 5) makes it logical to assume that nearly all the 1946 production came from the incoming 1943 year class and that practically all the 1947–48 production came from the 1943 and 1944 year classes. Since in most years fish of age-group III do not come into the catch until fall, the fall production in 1946 and the spring production in 1947 were considered to have come entirely from the 1943 year class. Production from the fall of 1947 and all of 1948 was apportioned between the 1943 and 1944 year classes in the same ratio as their contributions in 1949–53. The low production during the spring of 1946 and the poor representation in

TABLE 3.—*Commercial production (thousands of pounds) of walleyes in northern Green Bay, 1929–57*

Year	Production in gear					Total production
	Pound nets	Shallow trap nets	Fyke and hoop nets	Large-mesh gill nets	Other[1]	
1929	7	7	7	5	1	27
1930	6	5	13	3	—[2]	27
1931	14	5	20	2	1	41
1932	29	8	45	1	2	85
1933	37	18	53	—[2]	1	108
1934	26	17	61	—[2]	4	108
1935	18	11	27	1	—[2]	57
1936	29	17	25	3	—[2]	74
1937	10	17	28	4	—[2]	59
1938	4	9	25	—[2]	—[2]	38
1939	3	6	21	1	—[2]	30
1940	2	8	14	3	—[2]	28
1941	1	10	14	1	—[2]	26
1942	1	4	10	2	—[2]	16
1943	3	12	20	1	—[2]	36
1944	5	17	20	1	—[2]	43
1945	3	12	4	2	—[2]	21
1946	8	50	8	6	1	72
1947	41	148	24	48	1	262
1948	124	229	30	168	21	572
1949	161	421	33	436	12	1,063
1950	99	624	10	560	—[2]	1,294
1951	17	256	8	245	—[2]	525
1952	11	120	11	100	—[2]	242
1953	22	184	9	36	—[2]	252
1954	47	320	2	88	3	460
1955	42	549	—[2]	314	1	906
1956	15	423	—[2]	328	—[2]	766
1957	4	154	—[2]	93	—[2]	251

[1] Includes small-mesh gill nets, hook and line, deep trap nets, trolling, and unknown gear.
[2] Less than 500 pounds.

later samples indicated the 1942 and 1945 year classes were so weak that they could be ignored without significant effect on the estimates of year-class contributions in 1946–48.

Estimates of possible production from the 1951 and 1952 year classes in 1958 and 1959 were included to complete the production histories of the year classes. The ratio of the production of fish of age-groups V and VI from the 1951 year class was applied to the 1952 year class to estimate production at age VI. The regression from age V to VI was extrapolated for both year classes to estimate production at age VII. Estimates of the numerical catch per trap-net lift from these year classes in 1958 and 1959 (Table 10, Figure 5) were based on the assumption that fishing intensity would be the same in these years as in 1957.

Estimates of pounds and numbers have been rounded to the nearest thousand. It is not implied that all figures are correspondingly accurate.

COMMERCIAL FISHERY STATISTICS

The Green Bay walleye fishery is a multiple-gear fishery. Hile, Lunger, and Buettner (1953) have described the seasonal production and types of gear in use prior to 1951. Since 1945 the shallow trap net has been the most important gear in the fishery, but large-mesh gill nets (4½ inches and larger), pound nets, and fyke nets contributed substantially to the total production (Table 3). In 1949 gill nets produced more than any other gear, but since then the trap net has been the major producer. By 1950 the importance of fyke nets was declining, and after 1953 this gear was of little significance. After 1956 pound nets, too, almost disappeared from the walleye fishery.

The methods of handling statistical data on fishing intensity and abundance have been described by Hile (1937), Hile and Jobes (1941), and Van Oosten, Hile, and Jobes (1946). Hile, Lunger, and Buettner (1953) based their estimates of availability or abundance on records of catch per unit effort of pound nets, shallow trap nets, and fyke and hoop nets with 1929–43 as a base period. Their analysis of changes in the Green Bay fisheries extended through 1950. They were most skeptical of the estimates of fishing intensity and abundance for walleyes for the years 1947–50 and commented on the reason for their doubt. The numerous Lake Huron trap-netters who had moved to Green Bay used a larger and much more efficient type of trap net than was fished there prior to World War II. Fishing intensity for later years was, therefore, grossly underestimated, and abundance (ratio of actual catch to expected

TABLE 4.—*Production, fishing intensity, and abundance of walleyes expressed as percentages of the 1929–53 mean*

Year	Production	Fishing intensity	Abundance index
1929	13	36	47
1930	13	34	51
1931	20	34	76
1932	42	50	107
1933	53	38	180
1934	53	41	166
1935	28	38	95
1936	36	45	102
1937	29	40	94
1938	19	47	50
1939	15	40	48
1940	14	23	76
1941	13	17	95
1942	8	17	58
1943	18	21	108
1944	21	19	139
1945	10	27	48
1946	35	76	60
1947	128	170	96
1948	280	260	138
1949	521	396	168
1950	633	400	202
1951	257	270	122
1952	118	198	77
1953	123	164	96
1954	225	184	156
1955	443	256	222
1956	375	245	196
1957	123	119	132

catch) correspondingly overestimated. Inquiries of the local fishermen have since indicated this influx of former Lake Huron operators began as early as 1942 and that by 1945 most of the trap nets were of the larger type. This information made it possible to adjust the average catch per trap-net lift in the 1929–44 and 1945–53 periods according to the average abundance indices obtained from pound and fyke nets during these periods and thus to establish a continuity between the two periods for trap nets. The procedure for making this adjustment was described by Van Oosten, Hile, and Jobes (1946: p. 316). This type of adjustment is subject to some error. Old gears are usually used until worn out and changes in gear, although often rapid, are seldom, if ever, completed in one season. The adjustment permits estimates of intensity and abundance, however, that are far more closely descriptive of the fishery than those made without consideration of changes in gear.

Fishing with gill nets, despite occasional high yields, has not been included in the estimates of abundance. Some question exists as to whether the methods in the gill-net fishery have been stable for a sufficiently long period to establish a dependable base. Until the collapse of the whitefish fishery in 1955, gill nets were fished for whitefish and suckers as well as walleyes, but they are now fished principally for walleyes. Estimates have, therefore,

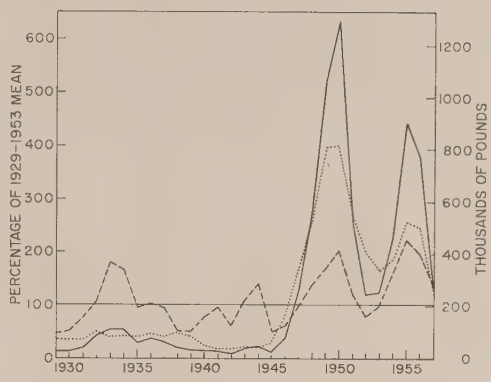

FIGURE 2.—Production (solid line), abundance (long dashes), and fishing intensity (short dashes) in the commercial fishery for walleyes in the State of Michigan waters of Green Bay, 1929–57. Scale at right applies to production; scale at left (percentages of 1929 53 mean) holds for all three variables.

been made from the same gears Hile, Lunger, and Buettner (1953) used, but the indices of intensity cover catches of all gears. The 1929–53 period is used as a base.

Production, fishing intensity, and abundance

Production of walleyes (Tables 3 and 4, Figure 2) in 1929–44 was much lower (generally well below 50 percent of the 1929–53 average of 204,000 pounds) than in the subsequent years. The catches of approximately 108,000 pounds in 1933 and 1934 (53 percent of average) were the highest in the earlier period. The catch fell to only 16,000 pounds (8 percent) in 1942, rose to 43,000 pounds in 1944, then fell again to 21,000 pounds (10 percent) in 1945. A 5-year period of rapidly increasing catch that began in 1946 led to a production of 1,294,000 pounds (633 percent) in 1950. A rapid decline during the next 2 years brought the catch down to 242,000 pounds (118 percent) in 1952. The next 5 years saw another increase to 906,000 pounds (443 percent) in 1955 and another decline to 251,000 pounds (123 percent) in 1957.

Fishing intensity (Table 4, Figure 2) was low throughout the 1929–44 period. It fluctuated between 34 and 50 percent of the 1929–53 average from 1929 through 1939, declined to less than 20 percent in 1941, and remained very low through 1944. An upward trend that began in 1945 ended in 1950 with an index of 400 percent. The intensity index fell to 164 in 1953, rose again to 256 in 1955,

TABLE 5.—*Production of walleyes (thousands of pounds), spring and fall*

Year	Season			Total
	Spring[1]	Fall[2]	Fall expected[3]	
1945	14	6	8	21
1946	15	57	28	72
1947	134	127	102	262
1948	343	229	224	572
1949	563	500	416	1,063
1950	939	355	506	1,294
1951	440	85	205	525
1952	179	63	95	242
1953	123	129	99	252
1954	218	242	180	460
1955	419	486	354	906
1956	618	148	300	766
1957	201	50	98	251

[1] January–July.
[2] August–December.
[3] 39 percent of annual catch (1945–57 average).

then declined to 119 in 1957, the lowest point in 11 years.

Abundance (Table 4, Figure 2), in contrast to production and fishing intensity, was moderately high during the 1929–44 period. Although the index was below 60 percent of average in 1929–30, 1938–39, and 1942, it was above 100 in 6 years and reached the 1929–44 high of 180 in 1933. Abundance was only 48 in 1945 but climbed steadily to 202 in 1950. It declined to 77 in 1952, rose to an all-time high of 222 in 1955, and dropped again to 132 in 1957.

The 1933 peak of production occurred during a time of high abundance and low effort, but the 1949–50 and 1955–56 peaks occurred during periods of high abundance and high effort. In view of the extremely high effort in 1949–50 and the resulting competition for the best grounds, it is possible the efficiency of the gear was not as high as during periods of lower intensity. The true abundance in those years may have been somewhat higher than the index indicates.

Production by season

The calendar year of fishing in Green Bay is divided conveniently into two periods of production. The earlier period runs from January through June and the latter from August through December. July, a month when the fishing is nearly always poor and the catch small, is assigned here to the "spring" production. It is believed that our spring and fall samples are reasonably representative of these periods. Since 1945 production has usually been greater in the spring than in the fall period (Table 5). Fall production averaged 39 percent (unweighted mean of annual percentage) of the annual total in 1945–57.

It appears that the relationship between actual fall production and the "expected" 39 percent of the annual total can be used as a rough index for prediction of production the next spring and the next year. In all years where fall production exceeded the expected percentage, production increased the next spring and *vice versa*. The correlation coefficient between actual deviations from "expected" fall production and changes in spring production the next year was 0.93 ($P < 0.001$). The relationship with production the next entire year is not as close but is good ($r = 0.65$; $p = 0.013$). Higher than "expected" fall production means either continued good take or better production than in the previous year. Lower than "expected" fall production indicates either continued low production or more likely a decline in the catch.

AGE AND YEAR-CLASS COMPOSITION OF THE SAMPLES

The information on age distribution (Table 6, Figure 3) includes actual determinations for available spring and fall samples of walleyes in 1949–58, and an estimate made by procedures described above for each spring or fall when sampling was missed.

The dominance of the 1949 and 1950 samples by the 1943 year class as age-groups VI and VII was extreme. In 1949, 88 percent, and in 1950, 72 percent of the fish sampled were from this year class. This powerful group persisted in the fishery until 1954 (age-group XI) in spite of the high fishing effort in 1948–51. The 1944 year class was small by comparison but remained in the fishery nearly as long as the 1943 fish. The 1945 and 1946 year classes obviously were very weak. The 1947 year class appeared to be moderately plentiful as age-groups III and IV but practically disappeared from the fishery after 1952. During the 1955–56 peak of production, three or four year classes were well represented in the samples in contrast to the one or two in the 1949–50 catch. The fish in the 1949–50 catches belonged principally to age-groups VI and VII, whereas those in the 1955–56 catches were considerably younger.

CONTRIBUTION OF AGE GROUPS AND YEAR CLASSES

To determine the contributions of the various age groups in the different years and seasons, the total weight of each sample was

TABLE 6.—*Percentage age composition in spring and fall samples of walleyes in Green Bay*

[Figures in parentheses are estimates as explained in Materials and Methods]

Age and season	Year of capture									
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
II										
Spring	–	–	–	–	–	–	–	–	–	–
Fall	–	–	–	–	–	–	–	–	4	–
III										
Spring	–	–	–	–	–	–	–	4–	2	1
Fall	1–	15	(4)	70	(54)	9	25	(7)	16	–
IV										
Spring	–	2	18	(7)	70	54	36	54	10	38+
Fall	2	1	(25)	2	(36)	58–	59–	(63)	14–	–
V										
Spring	4	–	2	(27)	–	36	60–	19	69	16
Fall	16	1	(3)	8	–	24	16	(18)	51	–
VI										
Spring	96	26	2	(5)	–	–	2	19	16	34+
Fall	80	11	–	1	(1)	–	–	(10)	5+	–
VII										
Spring	–	72	13	–	–	1	–	4	–	6
Fall	1	72	(12)	–	–	–	–	(2)	3	–
VIII										
Spring	–	–	65	(10)	3	–	–	–	1	2
Fall	–	–	(56)	3	–	–	–	–	1	–
IX										
Spring	–	–	–	(51)	8	–	–	–	2	1
Fall	–	–	–	16	(3)	–	–	–	–	–
X										
Spring	–	–	–	–	19	3	2	–	–	1
Fall	–	1	–	–	(6)	6	–	–	3	–
XI										
Spring	–	–	–	–	–	6	–	–	–	1
Fall	–	–	–	–	–	3	–	–	3	–
Number in sample										
Spring	109	57	46	–	37	70	47	141	258	151
Fall	171	158	–	222	–	33	57	–	74	–
Average age										
Spring	6.0	6.7	7.1	(7.3)	5.6	5.0	4.8	4.7	5.1	5.3
Fall	5.8	6.3	(6.6)	4.3	(4.0)	4.7	3.9	(4.4)	4.9	–

estimated as the sum of the products, number of fish in each age group times the average weight (grand average weights of Table 2). The ratio of the total commercial production in the season and year to the sample weight then gave a figure for the conversion of numbers and pounds in samples to numbers and pounds in the commercial catch. Determination of the total contribution of each year class required the summation of contributions at different ages and seasons.

The production by age groups (Table 7, Figure 4) illustrates the great strength and persistence of the 1943 year class. Its greatest contribution was at age VII, when nearly a million pounds were produced from this one group. The 1944 year class contributed its greatest poundage at age VI. Later year classes have all contributed their greatest weight at earlier ages (1947, IV; 1949–50, V; 1951–52, IV). The 1943 year class contributed 4.2 times the weight of the 1950 year class, 5.0 times that of the 1952 year class, and more than 200 times that of the weakest year class (1948). More than 3 million pounds were produced from this year class. This production is roughly 15 times the 1929–53 average annual production and 60 times the 1929–43 average, the former base for analysis of the fishery statistics.

The dominance of the 1943 year class over all others is well demonstrated by the percentages of the annual catches made up by each age group. In 1947 more than 90 percent of the production was 1943 fish. As late as 1952, when the year class was at age IX, more than half the catch was still from this group. The highest figure for any other year class is 67 percent for that of 1952 in 1957 (age-group V). No other group has made up more than half the catch at any age.

Numerically, the contribution of the 1943 year class overshadows that of any other (Table 8, Figure 4). Its numerical advantage is,

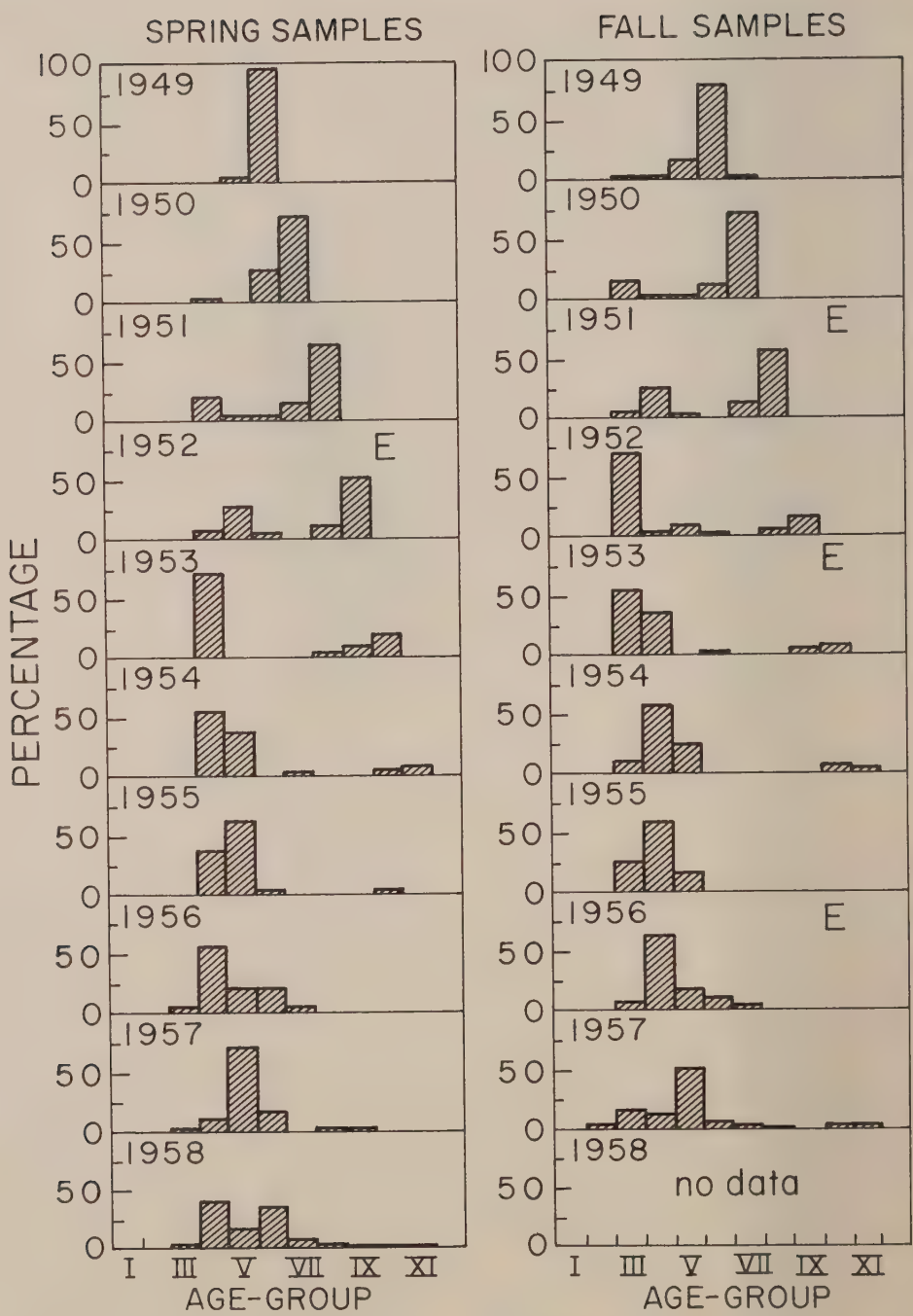

FIGURE 3.—Percentage age composition of spring and fall samples of walleyes in Green Bay. [Graphs marked "E" are estimates.]

TABLE 7.—*Weight contributions (thousands of pounds) to commercial production at each age, and total contributions to the fishery, 1943–1953 year classes of walleyes in northern Green Bay*

[Percentage of total in parentheses]

Year class	Calendar year												Total each year class
	1947[1]	1948[1]	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958[1]	
1943													
Age	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	–	
Pounds	241	480	951	986	374	138	77	51	–	–	–	–	3,355[3]
	(92)	(84)	(89)	(76)	(71)	(57)	(31)	(11)	–	–	–	–	
1944													
Age	III	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	
Pounds	21	92	96	268	75	21	24	54	–	–	–	–	651
	(8)	(16)	(9)	(21)	(14)	(9)	(10)	(12)	–	–	–	–	
1945													
Age	–	–	IV	V	VI	VII	VIII	IX	X	XI	–	–	
Pounds	–	–	7	4	10	–	4	–	27	–	–	–	52
	–	–	(1)	–[2]	(2)	–	(2)	–	(3)	–	–	–	
1946													
Age	–	–	III	IV	V	VI	VII	VIII	IX	X	XI	–	
Pounds	–	–	1	10	9	9	–	–	–	–	5	–	34
	–	–	–[2]	(1)	(2)	(4)	–	–	–	–	(2)	–	
1947													
Age	–	–	–	III	IV	V	VI	VII	VIII	IX	X	–	
Pounds	–	–	–	22	56	37	2	5	–	–	3	–	125
	–	–	–	(2)	(11)	(15)	(1)	(1)	–	–	(1)	–	
1948													
Age	–	–	–	–	III	IV	V	VI	VII	VIII	IX	–	
Pounds	–	–	–	–	1	8	–	–	–	–	7	–	16
	–	–	–	–	–[2]	(3)	–	–	–	–	(3)	–	
1949													
Age	–	–	–	–	–	III	IV	V	VI	VII	VIII	–	
Pounds	–	–	–	–	–	29	101	135	13	47	2	–	327
	–	–	–	–	–	(12)	(40)	(29)	(1)	(6)	(1)	–	
1950													
Age	–	–	–	–	–	–	III	IV	V	VI	VII	–	
Pounds	–	–	–	–	–	–	45	204	359	192	4	–	804
	–	–	–	–	–	–	(18)	(44)	(40)	(25)	(2)	–	
1951													
Age	–	–	–	–	–	–	–	III	IV	V	VI	VII	
Pounds	–	–	–	–	–	–	–	11	430	153	48	15	657
	–	–	–	–	–	–	–	(2)	(47)	(20)	(19)	–	
1952													
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	
Pounds	–	–	–	–	–	–	–	–	77	354	167	52	666[4]
	–	–	–	–	–	–	–	–	(8)	(46)	(67)	–	
1953													
Age	–	–	–	–	–	–	–	–	–	III	IV	–	
Pounds	–	–	–	–	–	–	–	–	–	21	7	–	—
	–	–	–	–	–	–	–	–	–	(3)	(3)	–	
Total annual production	262	572	1,063	1,294	525	242	252	460	906	766	251	–	—

[1] Estimates, explained in text.
[2] Less than 0.5 percent.
[3] Includes an estimated 57,000 pounds taken at age III in 1946.
[4] Includes an estimated 16,000 pounds taken at age VII in 1959.

however, not as great as its production advantage. Its numerical contribution was 3.2 times that of both the 1950 and 1952 year classes in contrast to 4.2 and 5.0 times, respectively, for the poundage contribution. The greatest numerical contributions from the 1943 and 1944 year classes were at age VI. The 1949 and 1950 year classes contributed most at age V and the 1951 and 1952 year classes at age IV.

The 1948–51 peak of production was supported almost entirely by the 1943 and 1944 year classes. Prior to 1951, more than 75 percent of the numerical catch was 1943 fish. The reduced production of 1952–54 was caused by the extreme weakness of the 1945, 1946, and 1948 year classes. The 1954–56 peak of production was sustained by four (1949 through 1952) year classes. Of the 1955 catch, 48 percent came from the 1951 year class and of the 1956 catch, 55 percent was from the 1952 year class. Because of the early disappearance of recent year classes from the fishery, only the 1952 year class contributed heavily (75 percent of the catch) in 1957, and, consequently, total production fell drastically (Table 3).

The average weight and age of a year class

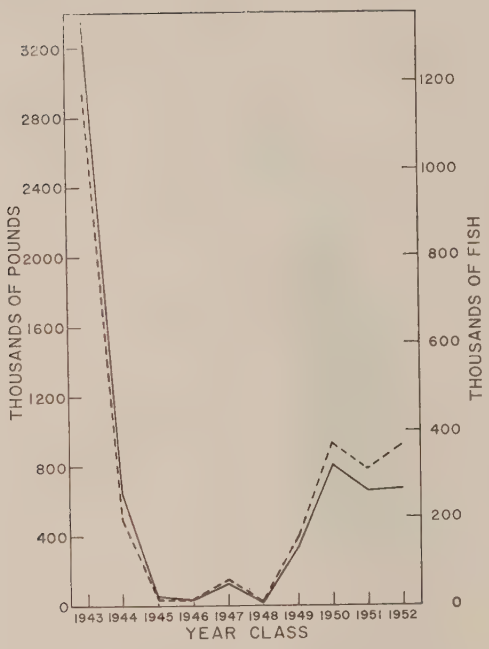

FIGURE 4.—Contributions to the fishery by the year classes of 1943 through 1952. Solid line, pounds; broken line, number of fish.

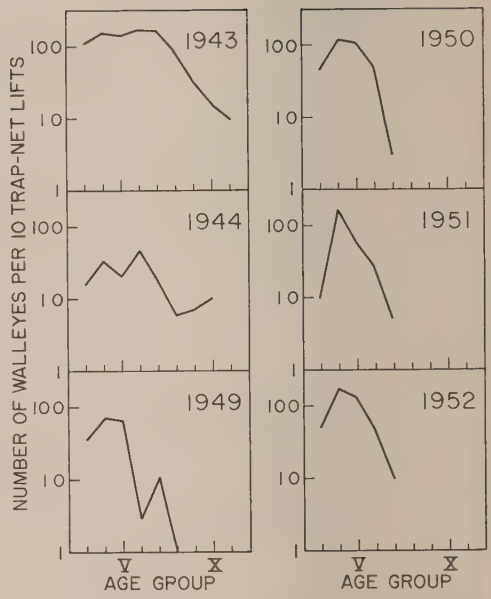

FIGURE 5.—Catch curves (number per unit effort on a log scale) of certain year classes of walleyes in northern Green Bay.

at capture (Table 9) have declined considerably during the years covered by this paper. The year classes of 1949 through 1952 averaged from 0.7 to 1.0 pound less at capture than the 1943 year class. The 1952 year class appears to have averaged less than two-thirds the weight of the 1943 year class at capture. This decrease in average weight is a direct consequence of the decrease in average age. Average age at capture of the 1943 year class was 1.4 to 2.4 years greater than that of the 1949–1952 year classes. The 1944 year class also averaged considerably heavier and older than more recent year classes.

ABUNDANCE OF AGE GROUPS AND YEAR CLASSES

The fluctuations in effort have been great enough since 1946 so that production summations are not a satisfactory index to strengths of year classes. Results of comparisons of year-class strength based on production summations (numbers of fish) can be affected greatly by the nature of the fluctuations of effort. If two equal-sized year classes are subjected to different or varying fishing rates, the one subjected to the greater effort during the years most closely following the age of significant or complete vulnerability will appear the larger of the two. High natural mortality intensifies this effect since more fish die of natural causes in groups where fishing mortality is low in earlier years.

Data on the numbers of walleyes of various age groups taken per unit of fishing effort provide a somewhat better basis for comparisons of year-class strength than do the summations of total numbers, but even these records offer certain troublesome problems of interpretation. If, for example, a year class enters the fishery during a period of intensive exploitation, its members may be cropped off so rapidly as they attain the 15½-inch minimum size that most have been taken well before the year class attains full vulnerability.[1] The catch per unit effort of the year class can be expected to decrease sharply soon after it

[1] The matter of vulnerability to the gear is of little consequence in this discussion since the principal impounding gears — trap nets, fyke nets, and the great majority of pound nets — have meshes small enough to hold any walleye of legal length. Large-mesh gill nets may not hold all 15½-inch walleyes, but the good agreement of age distributions in samples from gill nets and impounding nets suggests that escapage was small. Vulnerability is, therefore, used here to indicate attainment of legal size.

TABLE 8.—*Contributions to the commercial fishery (thousands of fish) at each age and total numerical contributions to the fishery by the 1943–1952 year classes of walleyes in northern Green Bay*

[Percentage of total in parentheses]

Year class	Calendar year												Total each year class
	1947[1]	1948[1]	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958[1]	
1943													
Age	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	–	
Number	132	209	327	297	115	33	12	9	–	–	–	–	1,173[3]
	(90)	(80)	(89)	(79)	(64)	(39)	(11)	(5)	–	–	–	–	
1944													
Age	III	IV	V	VI	VII	VIII	IX	X	XI	–	–	–	
Number	14	51	35	58	23	7	6	8	–	–	–	–	202
	(10)	(20)	(10)	(15)	(13)	(8)	(6)	(4)	–	–	–	–	
1945													
Age	–	–	IV	V	VI	VII	VIII	IX	X	XI	–	–	
Number	–	–	3	1	3	–	1	–	5	–	–	–	13
	–	–	(1)	–	(2)	–	(1)	–	(1)	–	–	–	
1946													
Age	–	–	III	IV	V	VI	VII	VIII	IX	X	XI	–	
Number	–	–	1	6	4	3	–	–	–	–	1	–	15
	–	–	–	(2)	(2)	(3)	–	–	–	–	(1)	–	
1947													
Age	–	–	–	III	IV	V	VI	VII	VIII	IX	X	–	
Number	–	–	–	15	33	17	1	1	–	–	–[2]	–	67
	–	–	–	(4)	(18)	(20)	(1)	(1)	–	–	–	–	
1948													
Age	–	–	–	–	III	IV	V	VI	VII	VIII	IX	–	
Number	–	–	–	–	1	5	–	–	–	–	2	–	8
	–	–	–	–	(1)	(6)	–	–	–	–	(2)	–	
1949													
Age	–	–	–	–	–	III	IV	V	VI	VII	VIII	–	
Number	–	–	–	–	–	20	54	58	5	15	1	–	153
	–	–	–	–	–	(24)	(51)	(31)	(1)	(4)	(1)	–	
1950													
Age	–	–	–	–	–	–	III	IV	V	VI	VII	–	
Number	–	–	–	–	–	–	31	105	164	67	1	–	368
	–	–	–	–	–	–	(30)	(55)	(38)	(18)	(1)	–	
1951													
Age	–	–	–	–	–	–	–	III	IV	V	VI	VII	
Number	–	–	–	–	–	–	–	8	207	72	17	5	309
	–	–	–	–	–	–	–	(4)	(48)	(19)	(16)	–	
1952													
Age	–	–	–		–	–	–	–	III	IV	V	VI	
Number	–	–	–	–	–	–	–	–	53	209	80	18	365[4]
	–	–	–	–	–	–	–	–	(12)	(55)	(75)	–	
1953													
Age	–	–	–	–	–	–	–	–	–	III	IV	–	
Number	–	–	–	–	–	–	–	–	–	15	4	–	—
	–	–	–	–	–	–	–	–	–	(4)	(4)	–	
Total annual production	146	260	366	377	179	85	105	189	434	378	106	–	—

[1] Estimates, explained in text.
[2] Fewer than 500 fish.
[3] Includes an estimated 39,000 fish taken at age III in 1946.
[4] Includes an estimated 5,000 fish taken at age VII in 1959.

first appears in the commercial landings. A year class that is fished lightly, on the other hand, may show an increase of numbers per unit effort over several years — as long as recruitment through attainment of legal size exceeds losses through fishing and natural mortality. We lack good information to judge the rate of attainment of legal size by Green Bay walleyes. Instructive, though not directly applicable, information on this point is given by the length–frequency data published by Hile (1954) for net-run samples of Saginaw Bay walleyes captured by small-mesh impounding nets in 1926–30. According to his records an occasional fish reached 15½ inches in three growing seasons but some females were still undersized at the end of five seasons and some males at the end of seven. Smith and Pycha (1961) also presented data on an extended period of recruitment in the gill-net fishery for walleyes in the Red Lakes, Minnesota. If the length of time between first and full vulnerability is equally large for Green Bay walleyes, interpretation of data on catch per unit effort of various age groups is uncertain to some degree.

TABLE 9.—*Average weight (pounds) and age (mean number of annuli) at capture of the 1943–1952 year classes*

Year class	Average weight	Average age
1943	2.86	6.1
1944	3.22	5.5
1945	4.00	7.2
1946	2.27	5.1
1947	1.86	4.1
1948	2.00	5.1
1949	2.14	4.6
1950	2.18	4.7
1951	2.13	4.4
1952	1.82	3.7

The first step in estimating the abundance of walleyes of different year classes at various ages required the use of sample data and records of trap-net production to calculate the numbers of walleyes of each age produced by trap nets in the spring and fall season of each year (see "Materials and Methods" for details of the procedure). Once the total for an entire year (sum of spring and fall estimates) was determined, the records of the annual number of trap-net lifts permitted computation of the number taken per lift for each age group. Since these numbers were sometimes small, the records of Table 10 are in terms of 10 trap-net lifts (Figure 5).

Fish of age-group III are, obviously, not fully vulnerable. Other age groups of the various year classes exhibit differences and trends that cannot be explained from the commercial fishery statistics. The slope of the survival curve for the 1943 year class indicates this group may not have been fully vulnerable until age VII or VIII although it entered the fishery as age-group III. Its maximum availability was as age-group VI or VII. The 1944 year class was most available as age-group VI. The 1949–1952 year classes were all most available as age-group IV although full vulnerability was undoubtedly at a later age for most of these year classes. The 1943 fish were still being caught in significant numbers at age X and XI, but the 1949–1952 year classes had all but disappeared by age VIII.

The early disappearance from the fishery and lower age of maximum availability of year classes more recent than that of 1946 points clearly to an increased total mortality among the later groups. Evidence is lacking for an increased natural mortality. Hile and Buettner (1959) gave evidence for their belief that the sea lamprey was the principal cause of the decline of the Saginaw Bay walleye in the middle and late 1940's. The situations in Saginaw Bay and Green Bay are, however, dissimilar. The decline of the walleye in Saginaw Bay followed closely the decline of the lake trout in Lake Huron. In Green Bay the abundance of walleyes was very high at the time the lake trout fishery had almost completely collapsed.

Neither can the increased mortality of the more recent year classes be traced to commercial operations. Fishing intensity (Table 4) has not increased but, on the contrary, has decreased. Fishing intensity was so high in 1948–51 (average index 331) as compared to 1954–57 (average index 201) that an increase, rather than a decrease, of average age and age of maximum availability would have been expected. A major increase in efficiency of the gear in recent years cannot properly be postulated as the cause of increased mortality. As was mentioned in an earlier section, the gear has not changed appreciably since 1946.

A marked increase in growth rate might account for recruitment at an earlier age, but not for an increase in fishing mortality after the fish have reached vulnerability. Evidence of a significant change in growth rate is lacking, however. Fish of the 1943–1944 year classes were nearly as heavy at corresponding

TABLE 10.—*Number of walleyes from each year class (1943–1952) taken per 10 trap-net lifts at each age*

Age	Year class									
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
III	111[1]	16[1]	–[1]	1	12	1	36	47	10	52
IV	154[1]	34[1]	2	3	27	4	71	124	173	177
V	141[1]	21	1	3	17	–	66	111	59	132
VI	168	48	2	3	1	–	3	52	27	46[1]
VII	166	18	–	–	2	–	11	3	5[1]	10[1]
VIII	87	6	2	–	–	–	1	–	–	–
IX	32	7	–	–	–	2	–	–	–	–
X	16	10	3	–	1	–	–	–	–	–
XI	10	–	–	2	–	–	–	–	–	–
Total	885	160	10	12	60	7	188	337	274	417

[1] Estimates; explained in "Materials and Methods."

ages as were those from the 1949–1952 year classes.

The sport fishery, on the other hand, is definitely known to have contributed to increased walleye mortality. The sport fishery developed mainly in response to the increase in abundance caused by the 1943 year class. In 1948 and 1949 angling was so good that many local anglers took out commercial licenses. In 1948 these "commercial" anglers averaged 60 pounds of walleyes per day and produced a total of 20,000 pounds. These figures represent only a small fraction of the sport-fishery production but offer good indication of the excellent quality of the fishing. The resort, dock, and boating facilities have been expanding so rapidly that even in the early and middle 1950's the scale of fishing must have been very large.

The first indication of the truly great magnitude of sport fishing for walleyes in Green Bay came from Eschmeyer's[2] report on a walleye tagging study initiated in September 1957 in northern Green Bay. The percentage return was low (a total of only 11.6 percent after two fishing seasons) as might be expected when a reward is not offered, but the comparative returns from anglers and commercial fishermen are pertinent to this study. Of 282 returns, 209 (74.1 percent) were from anglers and only 73 (25.9 percent) were from commercial operators. There is no reason to believe that one group of fishermen was more cooperative than the other in the return of tags. The lower returns from commercial operators are believed, therefore, to provide sound evidence that the sport fishermen took approximately three times as many tagged walleyes in 1958–59 as did commercial fishermen. The evidence suggests strongly, then, that the increase in mortality in recent years can be attributed to an increase in the intensity of the sport fishery.

The indication that the increase in mortality was caused by an increase in sport fishing further complicates the problem of estimating relative year-class strengths. Since the size limit for anglers is only 13 inches as against 15½ inches for commercial fishermen, a year class can suffer considerable reduction before it first becomes available to the commercial fishery. We therefore have no truly discriminating method for comparing the strength of year classes that were in the fishery during the early years of sampling with that of the more recent year classes. The problem, then, is finding the procedure that is least biased.

TABLE 11.—*Catch of walleyes of 10 year classes at age IV per unit effort of 10 trap-net lifts*

[Expressed as numbers of fish and as percentage of the 10-year average]

Year class	Number at age IV per unit effort	Percentage of average
1943	154	201
1944	34	44
1945	2	3
1946	3	4
1947	27	35
1948	4	5
1949	71	92
1950	124	161
1951	173	225
1952	177	230

Smith and Pycha (1961) used summations of the catch per unit effort at each age for an index to the strength of a year class. Their problem was to overcome differences in vulnerability to the gear at any one age caused by large annual fluctuations in growth rate. This procedure is of little use in a situation where total mortality has varied greatly as it has in northern Green Bay.

Under the circumstances that have been outlined, the best estimate of relative year-class strengths is probably made from a comparison of the numerical catches per unit effort of walleye at age-group IV, the earliest age at which most of the year classes had a substantial number of fish available to the commercial fishery. Even with this limitation the lower size limit for anglers will tend to make the estimates of the relative strength of the more recent year classes low. Annual fluctuations in growth rate could have affected the number of fish available at age IV in any year. Even though, as was explained earlier, we have no evidence of a truly large change of growth rate, the effects of small changes could have been material. To add further to the uncertainty are the small sizes of some samples and the fact that the numbers of IV-group fish of the 1943 and 1944 year classes are based on estimates. Estimates of relative year-class strength based on age-group IV fish (Table 11) accordingly must be viewed with some skepticism and interpreted with caution.

Despite the shortcomings of the data, the records of Table 11 do permit some definite conclusions. It is clear that the fluctuations of year-class strength of Green Bay walleyes

[2] Eschmeyer, Paul H. (1959) Great Lakes fishery research by the Michigan Department of Conservation, 1959. Report to the Upper Great Lakes Fishery Committee, Annual Meeting. (Multigraphed.)

have been enormous (well over fiftyfold). It is also clear that the original strength of such recent year classes as those of 1951 and 1952 matched or probably exceeded the strength of the extremely productive 1943 year class. The failure of recent strong year classes to attain their potential commercial productivity can be attributed to a fishing rate so high that they were eliminated at an early age and, hence, at a relatively small size.

IMPLICATIONS FOR FUTURE MANAGEMENT

The wide range of variability of year-class strength and the considerable number of years that may separate the appearance of strong year classes suggest that wide fluctuations of abundance and production will continue to characterize the walleye fishery of northern Green Bay. The effects of this variability have been heightened in recent years by an increase of fishing mortality that eliminates each incoming year class at an early age.

Any attempt to stabilize abundance and production by spreading the exploitation of a year class over a longer period of years must be based on a lowering of fishing mortality. Inasmuch as evidence now available indicates that the increase of mortality came about through a great expansion of sport fishing and that anglers take many more walleyes than do commercial fishermen, we must look principally toward regulations of angling if any substantial reduction in fishing mortality is to come about. Relatively little can be gained from further restrictions on the already stringently regulated commercial fishery.

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A Challenge to the Fish Meal and Oil Industry in the Gulf of Mexico

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THE CLUPEOID OR HERRING-LIKE FISHES constitute the most abundant fishery resource used by man and account for nearly one fourth of the world's total fish production. Historically the herrings have been utilized directly as food, but in recent years these fishes have achieved greater importance as the principal raw material of the fish meal and oil industry. The distribution of these fishes is worldwide. Most of the numerous species in the group occur in the ocean where they are principally confined to the coast or at least are not concentrated far from shore.

There are other important characteristics which make the herring-like fishes particularly desirable to the fish meal and oil industry (1) Most of these fishes normally occur in dense schools. Furthermore, they generally school by species, and the individual schools usually consist of fish which are fairly uniform in size. These schooling characteristics facilitate mass production methods of catching, handling, and processing. (2) The herrings are plankton feeders and thus form one of the early links in the food chain; consequently they are among the most numerous fishes. The menhaden, for example, is one of the few fishes that feeds directly on the basic food producer in the ocean and thus represents a two-link food chain—the shortest possible and uncommon among the fishes in the sea. (3) They grow rapidly and reach maturity early; consequently many species can be utilized at the end of their first year of life and probably afford the maximum yield by the end of their second or third. (4) Many of the clupeoids undertake seasonal and annual migrations which lead them into areas where they can be conveniently caught. (5) Fishes in this group are relatively high in protein and body fat.

Because of these and other characteristics, there is little doubt that the clupeoid fishes in the Gulf of Mexico constitute the most promising resource, yet of the 25 generally recognized species in this group which occur in the Gulf and contiguous waters, only two—the Gulf menhaden, *Brevoortia patronus*, and the anchoveta, *Cetengraulis edentulus*—are being utilized by the fish meal and oil industry.

In the search for basic knowledge of the species which constitute the menhaden resource and their distribution in time and space, several survey trips were made along the southeast coast of the United States during late 1958 and 1959. Results revealed that the stocks along the Atlantic and Gulf coasts were not isolated and separated from each other as believed, but were distributed continuously around the Florida peninsula (Reintjes, 1960). This

finding showed that the distribution of these fishes in the Gulf of Mexico was much greater than was reported. During the past year, therefore, efforts were directed toward the collection of the various species of menhaden in coastal waters from Fernandina Beach, Florida, on the Atlantic coast to the Gulf of Campeche. A second objective of the field work was to obtain information on the distribution and relative abundance of other herring-like fishes of potential value to the fish meal and oil industry.

Based upon field observations, discussions with fishermen and processing plant operators, and extensive collections, it was obvious that the clupeoid fishes in the Gulf of Mexico are much more widely distributed and occur in greater abundance than previously known.

The primary purpose of this paper is to summarize present information on the range, relative abundance, and seasonal occurrence of several species in the hope that it may stimulate exploration and subsequent utilization by the fish meal and oil industry.

The Gulf menhaden at present is the more important of the two species being utilized. Juveniles occur in schools in the open waters along the Gulf coast from Mexico to southern Florida. Larvae appear in salt-water lagoons and estuaries along the Gulf coast during the winter months, and young-of-the-year juveniles are encountered in these same areas throughout the summer. This species supports the commercial purse-seine fishery which is conducted generally from mid-April to mid-October in the vicinity of Apalachicola, Fla., and along a relatively short stretch of coast lying between Alabama and Texas. Samples from the catches indicate that the fishery is based on 1- and 2-year-old fish. Older, sexually mature fish are generally absent from the catches. Collections from southern Florida and Mexico (southward to Yucatan) have shown that during the summer adults increased in size toward the southern limits of the range; however, the abundance of both juveniles and adults appeared to diminish. The occurrence of large, adult Gulf menhaden in southern Texas and in the vicinity of Veracruz in mid-summer suggests a greater abundance of this species in the southern Gulf of Mexico during the winter when it disappears from more northerly waters. It also is of interest to note that spawning adults of this species were taken during the past two winters off the east coast of Florida, and some of the catch in the Indian River area this fall has consisted of large, spawning adult fish provisionally identified as Gulf menhaden. These averaged about 10 inches in length. In summary, present information indicates that either this species has an unusually short life-span, which based on present information appears unlikely, or the adult segment of the population is not being utilized by the fish meal industry. If the older, larger fish exist in concentrations—and we believe that they do—and if these could be located and caught, they could appreciably increase the yield and afford a greater economic return than is now being realized from the species population.

The finescale Gulf menhaden is known to occur from eastern Louisiana to the Gulf of Campeche (Christmas and Gunter, 1960) and there is evidence to suggest that it extends around the Yucatan Peninsula and into the Caribbean Sea. This species does not occur in abundance in purse-seine catches; however, individual landings consisting entirely of finescale Gulf menhaden have been reported in western Louisiana waters and off Campeche. This past summer, large adults were present in beach-seine, gill-net, and shrimp-trawl landings

along the entire Texas coast. Since none of these gears is adapted to catching menhaden, even in areas of known abundance, their occurrence in the catches is of significance. Juveniles of this species also were obtained as far westward as the Laguna Madre of Texas. It is concluded that this species constitutes an unknown resource which apparently occurs in greatest abundance from Corpus Christi, Texas, to the lower Gulf of Campeche.

Yellowfin menhaden are distributed continuously from the central east coast of Florida to the delta of the Mississippi River. A gill-net fishery for this species for bait purposes is conducted throughout the year in Indian River, Florida. Landings in recent years have averaged about 325,000 pounds, and the fish have been available throughout the year. Fish in the catches are consistently large, ranging from about 8 to 12 inches in length. Adults of this species also have been caught by gill nets in Florida Bay near Marathon during the winter and off Naples in early spring. Eggs, larvae, and juveniles of this species have been collected in Indian River, and juveniles have been encountered in abundance in estuaries near Everglades City, Naples, Punta Gorda, and in Tampa Bay, Fla. It appears that the areas of greatest abundance of yellowfin menhaden are from Cape Canaveral to St. Lucie Inlet on the Atlantic side and from Cape Sable to Sarasota, Fla., in the Gulf of Mexico. The whereabouts of the younger adults are unknown, yet it probably is this segment of the species population which offers the greatest potential to the fish meal and oil industry.

The thread herring, *Opisthonema oglinum*, occurs generally throughout the Caribbean and along the Gulf coastal states southward to the Gulf of Campeche. This species was found to be available in large quantities throughout the year along the west coast of Florida and appeared to be present in large numbers in the shallow coastal waters of the remaining Gulf states during the summer. Based on surface school observations and the results of experimental fishing by Bureau's exploratory vessel M V *Oregon*, it has been estimated that this species is more abundant than the Gulf menhaden. It can be caught with standard menhaden purse-seine gear since substantial landings are made each fall at Beaufort and Southport, N.C., when schools are encountered in the shallow waters along the shore. The oil yield at that time of year generally exceeds that of menhaden of comparable size. The fish reach a maximum length of about 12 inches.

Several species of anchovies occur along the Gulf coast and through the West Indies. The most abundant species appeared to be the bay anchovy, *Anchoa mitchilli*, which is distributed in the northern and western Gulf to Texas where surface schools are available from early spring through late autumn. Indeed Gunter (1945) has estimated this to be the most numerous species in Texas coastal waters. The anchoveta, *Cetengraulis edentulus*, occurs in quantity in southern Gulf of Mexico and is the principal species presently being exploited by the purse-seine fishery in the Gulf of Campeche.

Other clupeoids such as the scaled sardine, *Harengula pensacolae;* Atlantic round herring, *Etrumeus sadina;* and the Spanish sardine, *Sardinella anchovia*, may also exist in mid-water depths in commercial quantities, but there is little precise knowledge of their seasonal distribution and relative abundance.

The Bureau's Pascagoula, Miss., Exploratory Fishing Base has gathered a wealth of information on the geographical distribution, seasonal occurrence and relative abundance of the Gulf clupeoids. These catches are being examin-

ed in detail for species identification and length, weight, and maturity condition of the fish. The Bureau's Biological Laboratory at Galveston also is gathering information on those clupeoid species which appear in the industrial trawl fishery conducted in the northern Gulf. Summaries of these data will be of great value to those individuals within the fish meal and oil industry who are interested in locating and exploiting new stocks of fish.

It is recognized that many of the shallow waters close to shore are known and, to a large extent, are being exploited by the present purse-seine fishing fleets, but it also appears that, either because of gear limitations or lack of exploration, there occur in these same areas commercial concentrations of fishes suitable for reduction into meal and oil which are not being utilized. It also is recognized that there are many practical problems which tend to limit or discourage a systematic program of new resource development, but it also must be pointed out that once the biological potential is recognized that, because of its trained personnel, equipment, and facilities, the industry is in the best position for making a complete appraisal of the economic potential of the resource, from the development of efficient methods of capture to the processing of the raw material. Most of the crews, vessels, and plants are idle during the winter months when they could be utilized for these purposes.

If further development of the clupeoid resource in the Gulf of Mexico is contemplated, the following may serve as useful guidelines:

(1) Exploratory fishing should be conducted to ascertain the whereabouts of Gulf menhaden during the winter months and determine whether fish larger and older than those presently being caught exist in concentrations within the region. The most likely places of occurrence appear to be along the southern coast of Florida and along the eastern coast of Mexico.

(2) Initial utilization of the yellowfin menhaden population probably should be attempted during the winter months in the vicinity of the Indian River and along the southwest coast of Florida.

(3) Initial efforts to locate the finescale Gulf menhaden population probably should be attempted along the south Texas coast and the Gulf of Campeche.

(4) Until considerably more information is available, the potential of the yellowfin and finescale Gulf menhaden resources should be considered much smaller than that of the Atlantic and Gulf menhadens.

(5) Winter capture of menhadens, anchovies, scaled sardine, and other clupeoids probably will require the development of fishing methods and equipment somewhat different from those presently employed by the menhaden purse-seine fishery. Possibly auxiliary boats employing lampara or small-mesh purse seines or mid-water trawls would be most satisfactory in the company of large refrigerated menhaden vessels serving as carriers. The exploratory fishing staff at Pascagoula, Mississippi, is working on the problem of gear design.

(6) The thread herring resource appears to offer the greatest potential as an additional source of raw material during the winter. The most likely area for initial exploration is along the west coast of Florida.

In summary, the work conducted during the past several years has demonstrated that number of the clupeoid fishes are more widely distributed in the Gulf of Mexico than was believed, and it probably is the winter concentrations of the several species mentioned which offer the greatest challenge to the fish meal and oil industry.

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Sei Whales with Rudimentary Baleen

by

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The baleen whales are highly specialized, both in structure and behavior, for filter-feeding on plankton. The primary structures involved in filter-feeding are the baleen plates. It would thus seem impossible for these whales to survive if they lacked baleen. During the whaling seasons of 1959 and 1960, I examined 39 sei whales *(Balaenoptera borealis)* taken near the Farallon Islands by the Golden Gate and Del Monte whaling stations of Richmond, California. Among these whales I found two which almost completely lacked functional baleen, and a third which lacked functional baleen on one side. In each abnormal baleen row, most or all of the plates were rudimentary (fig. 1). They were 2 to 7 centimeters long, and lacked all traces of fringe. Their free edges were very irregular, «ragged», and deeply cut, giving the palate somewhat the appearance of being densely covered with innumerable long papillae. The plates were abnormally thick and soft; they were readily torn and pulled from

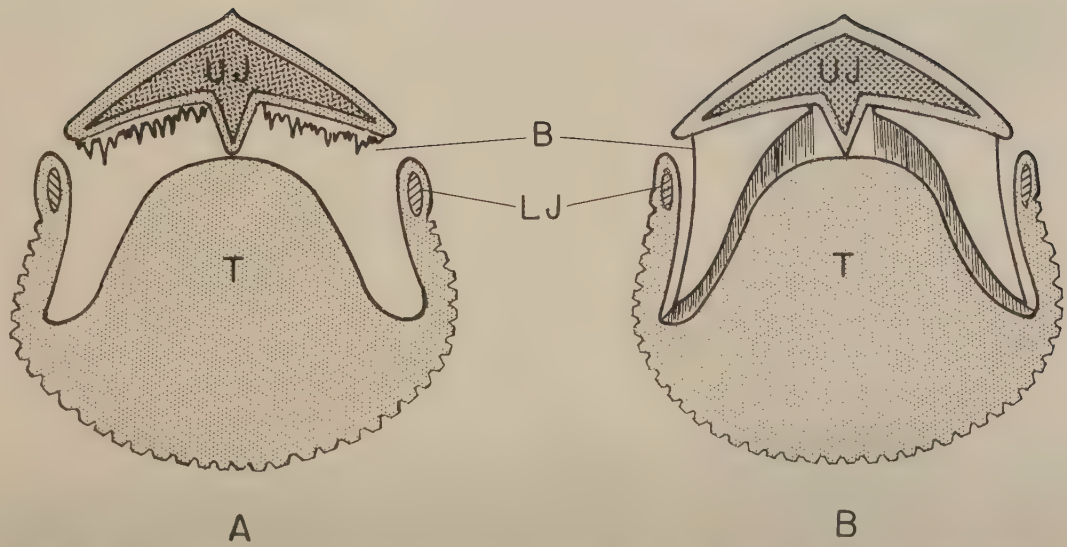

Figure 1. Diagrammatic cross section through mouth of a sei whale with abnormal baleen (a), compared with that of a normal sei whale (b). UJ — upper jaw; LJ — lower jaw; T — tongue; B — baleen.

the gums. When a few normal plates were present in the same row, the transition from rudimentary to normal plates was abrupt.

Data on the three abnormal whales are as follows:

No. 40. — Killed 12 June 1959. Male, 14.0 m. long. Ear plug with 21 laminations (probable age 10 years). Left testis 2.2 kg., right 1.9 kg. Stomach full of northern anchovies *(Engraulis mordax);* blubber thickness 5 cm. on back and belly, 4 cm. on side. Baleen rudimentary except for posterior 56 plates on right side which were normal.

No. 245. — Killed 13 August 1960. Male, 13.1 m. long. Ear plug with 26 laminations (probable age 13 years). Left testis 4.7 kg., right 4.8. Stomach empty. Blubber thickness 10 cm. on back, 7 cm. on belly, 6 cm. on side. Baleen rudimentary except for posterior 40 plates on left side, which were normal.

No. 246. — Killed 13 August 1960. Female, 13.7 m. long. Ear plug with 28 laminations (probable age 14 years). Ovaries with five corpora albicantia; lactating, not pregnant. Blubber thickness 9 cm. on back, 8 cm. on belly, 5 cm. on side. Stomach full of northern anchovies. All baleen plates on left side and anterior 30 plates on right side rudimentary.

It is not known whether the rudimentary condition of the baleen plates is genetic, or due to injury or disease. That two abnormal whales (Nos. 245 and 246) were killed the same day from the same school suggest either a genetic mutation or a contagious infection. It is difficult to imagine an injury that could mutilate part of baleen row without affecting adjacent plates; possibly a prenatal or very early postnatal injury could be responsible.

Calanoid copepods and euphausiids are the

chief foods of sei whales in most areas. In the waters of California, sei whales also eat many fish (northern anchovies; and Pacific sauries, *Cololabis saira)*. The three whales listed above could not feed on copepods or euphausiids, because filter-feeding would be impossible. The few normal baleen plates of whales No. 40 and 245 were too far back in the jaw to function as filters. Nor could whale No. 246 feed effectively by filtering, because most of the plankton would be lost through the left side of the mouth. These whales could capture anchovies only by grabbing and holding them between the tongue and palate. The extremely rugose edges of the rudimentary baleen would greatly aid in holding the fish. Probably very few fish could be captured at a time, yet two of the whales had full stomachs and all had blubber of normal thickness for sei whales at this season in these waters.

Miller (1929; Proc. U. S. Natl. Mus., 74 (26): 1—4) has shown that the grasping «gum-teeth» on the palate of the porpoise *(Phocoenoides dalli)* are histologically similar to embryonic baleen, and he implies that baleen plates may be derived (phylogenetically) from analogous structures. Perhaps the atrophied baleen of these sei whales is similar to that of the earliest mysticetes. If so, we have an indication of the ancestral feeding habits which led to the evolution of the highly efficient filter-feeding apparatus of modern baleen whales.

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SANDEFJORD

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Census of the California Gray Whale, 1959/60

By

Dale W. Rice

(U.S. Fish and Wildlife Service)

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A census of the California population of the gray whale *(Eschrichtius gibbosus)* was conducted at Point Loma, California, during the 1959/60 southward migration, by the U. S. Fish and Wildlife Service in co-operation with the National Park Service. The purpose of this census was to determine population trends in the gray whale population. This work is a continuation of the gray whale census program started by Gilmore in 1952/53, and carried on by him through the 1956/57 season (Gilmore, 1960a, 1960b).

Methods

The census was conducted at the Cabrillo National Monument, at the summit of Point Loma, San Diego, California. The methods were essentially those employed by Gilmore *(op. cit)*, whose report should be consulted for a detailed description. The project was under the direction of the writer; other observers included William V. Martin for the Fish and Wildlife Service, and Francis R. Holland, Richard Knowles, Donald M. Robinson, and Theodore Walker for the National Park Service.

An observer, equipped with 7×50 binoculars, was stationed in the lookout bunker continuously from 0700 until 1700 (essentially sunrise to sunset) every day from 14 December to 22 February. All groups of whales were carefully observed; the number in each group and the hours of passage were recorded.

Results

The daily counts are presented in the accompanying graph (fig. 1). The total for the period 10 December to 22 February was 2,344.

In attempting to calculate the total population from this data, three extrapolations must be made (Gilmore, *op. cit.)*:

1. *Whales missed because of poor visibility, etc.* It is difficult to estimate the number of whales which the observers miss. Gilmore *(op. cit)* estimated the proportion that visibility was reduced by fog or rough weather and used this estimate to calculate the total number which probably passed each day. This was deemed impractical during the 1959/60 census for two reasons: (1) The estimate of reduced visibility is largely subjective and evaluations by different observers often do not agree. (2) Weather conditions change so rapidly, even within the hour, that it is virtually impossible to determine an average visibility reduction factor for an entire day.

Instead, a different method was used. A smooth curve, connecting the days with better weather and higher counts, was drawn freehand on the graph of daily counts (fig. 1). From the graph area included within the curve, the total number of whales passing Point Loma during daylight hours was estimated at 3,400. Undoubtedly, this method gives too high an estimate for some days; conversely, it does not take into account the fact that some whales are missed, even on the days with good visibility. Although this method is crude, no data are available for improving it.

2. *Whales passing at night.* Gilmore *(op. cit.)* presents evidence which suggests, that migration is slowed at night to about half the daytime rate. On this basis, the total number of whales which passed Point Loma during the 14 hours of darkness each night may be estimated at 0.7 of the estimated total for the 10 daylight hours, or 2,300. This is probably a minimum figure.

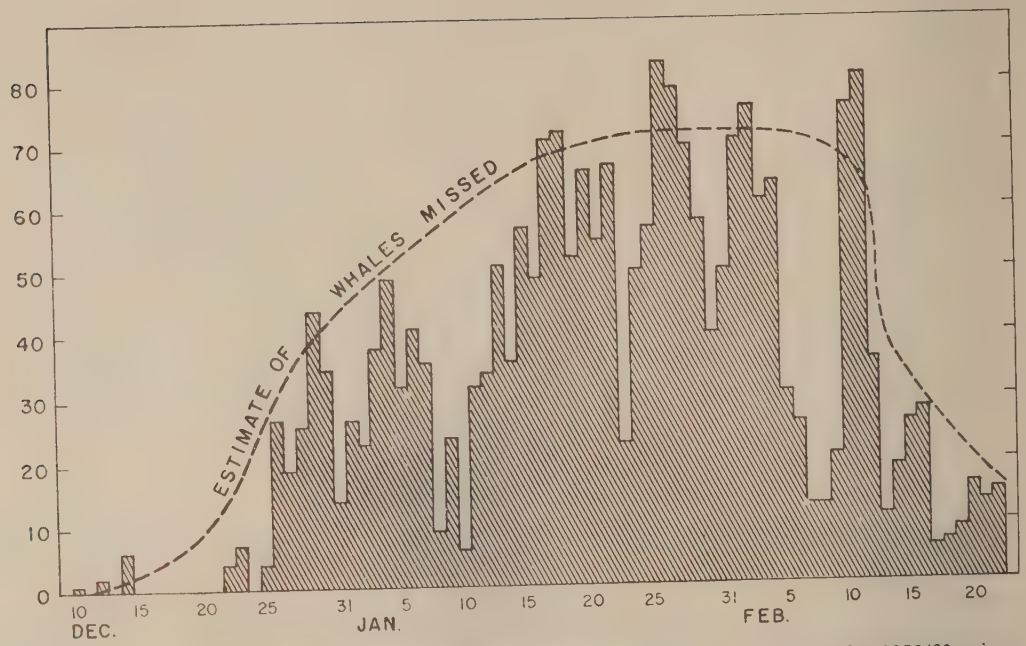

Figure 1. — — Daily counts of southbound gray whales at Point Loma during the 1959/60 migration . A number were missed because of fog, rough seas, etc.; the estimated totals for days with poor visibility are indicated by the dashed line.

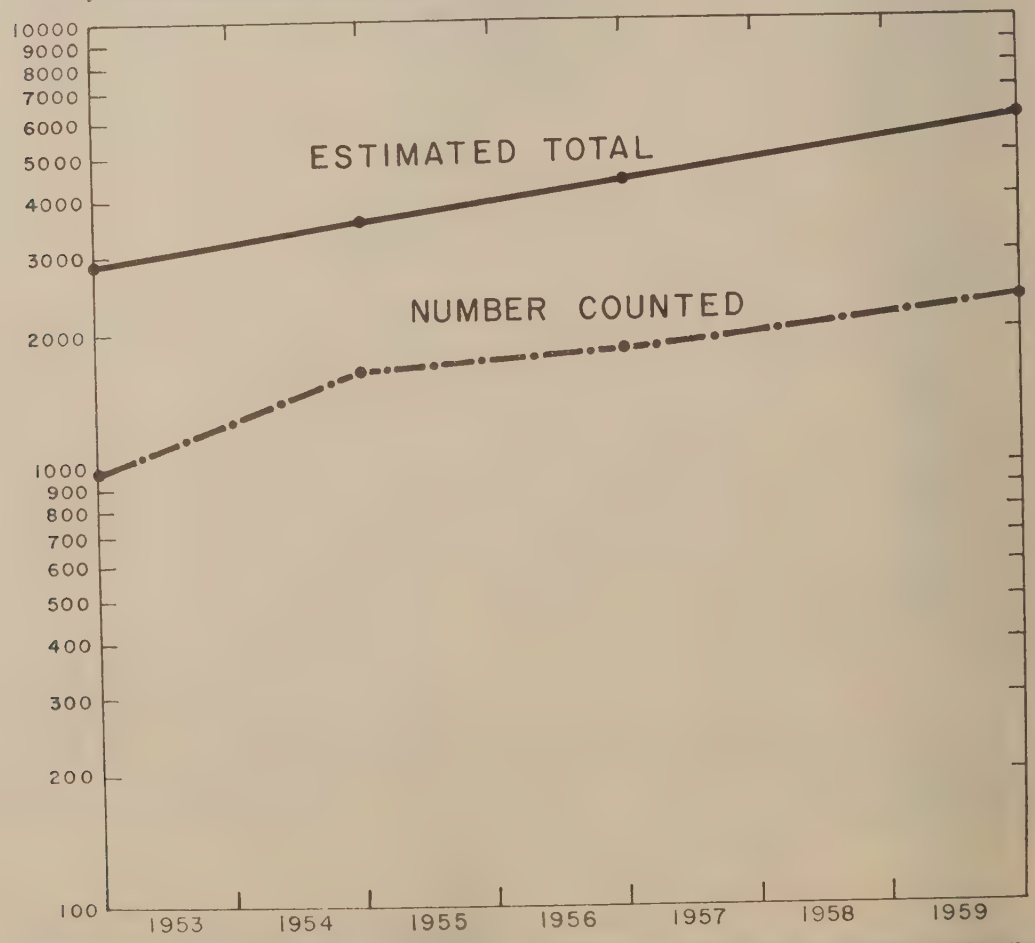

Figure 2. — — Actual counts, and estimated total population of California gray whales during the southward migration 1952/53 through 1959/60 seasons.

3. *Whales passing far offshore.* This was arbitrarily estimated at 5 percent of the total inshore migration by Gilmore *(op. cit.)*.

The results of these extrapolations give us a total population estimate as follows:

	Number
Daily count	2,344
Estimated number missed	1,056
Estimated number passing at night	2,380
Estimated number passing offshore	289
Estimated total population	6,069

Accuracy of Estimate

Since the extrapolation must be based on somewhat arbitrary assumptions, the probable minimum and maximum population sizes have been estimated.

To determine a minimum figure, the extrapolations for whales missed during daylight hours, and for whales migrating offshore, have been eliminated, giving a result as follows:

	Number
Daily count	2,344
Estimated number passing at night	1,640
Estimated minimum total	3,984

Figure 3. — —Aerial view (looking south) of Point Loma, California, site of Cabrillo National Monument. Migrating whales travel down the west side (right) of the point, usually 0.5—3.0 km. offshore, and round the point heading southeast (upper left) towards Baja California. The whale lookout («A») is 130 m. above sea level. The many automobiles show how many visitors the whale migration attracts.

A maximum figure was calculated by assuming that night migration proceeds at the same rate as daylight migration. This would add another 2,380 to the estimate of 6,069, for a total of 8,449. The offshore migration may also be larger than the estimated 5 percent. However, it seems, from available information, improbable that the population can be much greater than 9,000.

When compared with the previous years' counts, a continued steady increase in the population, at a rate slightly above 10 percent per year, is indicated (fig. 2).

Although the estimates of total population are subject to a wide margin of error, the high degree of consistency in calculated rate of increase from year to year indicates that the census provides a reliable index of relative numbers from one year to the next.

Discussion

The original population of the California gray whale, in 1853—1856, was estimated as «probably not over 30,000» by Captain Scammon (1874), a careful observer with much experience. Between 1846 and 1874, about 10,800 gray whales were killed in California and Baja California; very few were killed on the arctic summer grounds (Scammon, *op. cit.)*. In 1874, Scammon *(op. cit.)* estimated the population at 8,000 to 10,000.

The population remained low until recent years, when the protection afforded by the International Convention for the Regulation of Whaling has permitted them to increase.

If estimates of past populations are sufficiently accurate to be an indication of the carrying capacity of the range, a further four- to five-fold increase in the California population would seem possible.

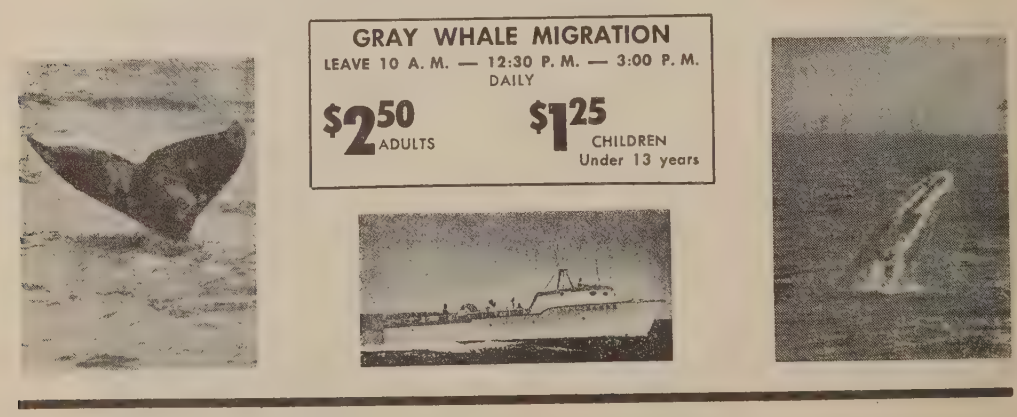

Figure 4. — — Advertising brochure for gray whale sight-seeing cruises (name of firm deleted).

If the present rate of increase continues, the population theoretically would approach this number in about 15 years. (In actuality, it will probably take longer as the rate of increase in wild mammalian populations tends to decrease as the carrying capacity is approached.)

In recent years, there has been some thought of permitting a commercial take of gray whales. In order to obtain the highest sustained yield, the population should be allowed to grow to near maximum size before being opened to regular whaling operations. By analogy with studies on fin whales (Ottestad, 1956), a population approaching 30,000 animals should be able to sustain an annual kill of 5 percent, or 1,500.

At present, the esthetic value of the gray whale is of major importance. During the whale migration, thousands of visitors daily visit the Cabrillo National Monument to watch the migrating whales (fig. 3). During 1959, the Monument was host to over 999,000 visitors (more than the Statue of Liberty and ranking second as compared with all U. S. national monuments), many of whom came specifically to see the whales. Nowhere else in the world is it possible for the general public to observe at close range the mass migration of one of the world's largest mammals. During the 1959/60 season, three sportfishing companies (two on San Diego Bay and one on Mission Bay) operated regular «whale-hunt» cruises (fig. 4). By approaching the migrating whales from the north, they are able to follow the whales as closely as 30 meters without unduly disturbing them, giving the passengers excellent close-range views and opportunities to take photographs. In managing the gray whale, its commercial value should be regarded as secondary to its esthetic value.

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Observations on the Habits of the Whalesucker *(Remilegia australis)*

by

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and

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(Los Angeles County Museum)

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(Remilegia australis)

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The whalesucker (*Remilegia australis* Bennett, 840) (Fig. 1), a member of the remora, or suckerish, family (Echeneididae), is apparently an bligate commensal of cetaceans. It is the only emora known to utilize cetaceans as hosts. lthough widely distributed throughout the tropcal and temperate Atlantic, Pacific, and Indian)ceans (Follet and Dempster, 1960), it is rarely ollected. Its rarity may be more apparent than eal. Virtually nothing has been published conerning its habits. While studying whales taken in he waters off California during 1959 and 1960, Rice made observations on living whalesuckers, oth at sea and in the whaling stations. Caldwell dentified the whalesuckers and examined their tomach contents.

Hosts.

Follet and Dempster (1960) summarized the ublished host records. These included only four pecies: blue whale (*Balaenoptera musculus* Linn., 758); sperm whale (*Physeter catodon* Linn., 1758); ommon dolphin (*Delphinus delphis delphis* Linn., 758 and *D. d. bairdi* Dall, 1873): and spotted dolhin (*Stenella plagiodon* Cope, 1866). Many pubished reports do not identify the host.

Rice observed them on blue whales and on sei vhales (*Balaenoptera borealis* Lesson, 1828). Loyd Newton, a whaling captain with many years' xperience off Peru and California, and Gilbert Hunter and Grant Yost, who have whaled for severl years off California, have regularly observed remoras on blue whales. They have not observed them on other species of whales taken in the same waters at the same time. Harold Ridle, a catcherboat captain who has whaled off San Francisco for two years, believes he has seen them on fin whales (*Balaenoptera physalus* Linn., 1758) and humpback whales (*Megaptera novaeangliae* Borowski, 1781). This requires confirmation. Rice has examined many fin whales and humpback whales, and a few sperm whales, giant bottlenose whales (*Berardius bairdi* Stejneger, 1883), and gray whales (*Eschrichtius gibbosus* Erxleben 1777), without finding remoras.

Frequency of Occurrence.

Remoras were found on three of the five blue whales captured during the 1959 whaling season, and examined at the whaling stations. The number of remoras per whale was 1, 3, and 4. Remoras doubtless tend to become disengaged from a dead whale while it is being towed into the station, a trip of 6 to 12 hours. According to the crew members of the catcher boats, almost every blue whale taken in California and Peruvian waters has remoras — from three or four to more than a dozen. Most are about 15 cm. long, a few are up to 50 cm. long.

In contrast, they are infrequently found on other cetaceans. Rice observed at least nine whalesuckers (10 to 20 cm. long) on one of three sei whales killed from a school of seven on 4 September 1960.

Behavior.

The remoras may be attached at almost any point on the whale's body. On freshly killed whales at sea, they cling to the smooth back and sides, and avoid the grooved throat region to which they perhaps have difficulty in clinging. Remoras collected from blue whales were on the dorsal surface of the rostrum (1 specimen); on the posterior portion of the right upper lip adjacent to the baleen plates (4 specimens); and on the side of the anterior thoracic region (3 specimens).

Some of them clung to the emerged portions of a dead sei whale for almost an hour, and made no effort to move to the submerged portions. When waves washed over them, they held the posterior parts of their bodies limp, so that they offered least resistance to the water.

All remoras observed on dead whales in the whaling stations were oriented with head pointed towards the whale's tail. This was doubtless because the dead whales are towed tail-first by the catche boats. On living and recently dead whales, the were oriented with head pointed toward the whale' head. Remoras on a freshly killed sei whale oriente in the same direction as the whale was movin while the latter was being winched head-first to wards the catcher boat. After the whale wa secured alongside the boat, head toward the stern the boat got underway at about 14 km. per hou At this time the remoras reoriented themselves wit head toward the bow. They remained attached t the whale for several hours, but all dropped off be fore the boat reached the whaling station 9 hour later. The speed of the towing vessel could hardl be responsible for their dropping off, because it di no greatly exceed the normal swimming speed c sei whales, and is far below their maximum speed. 50-cm. remora was observed clinging to (and eve shifting position on) a dolphin swimming at 17 km per hour (Mahnken and Gilmore, 1960). Perhap

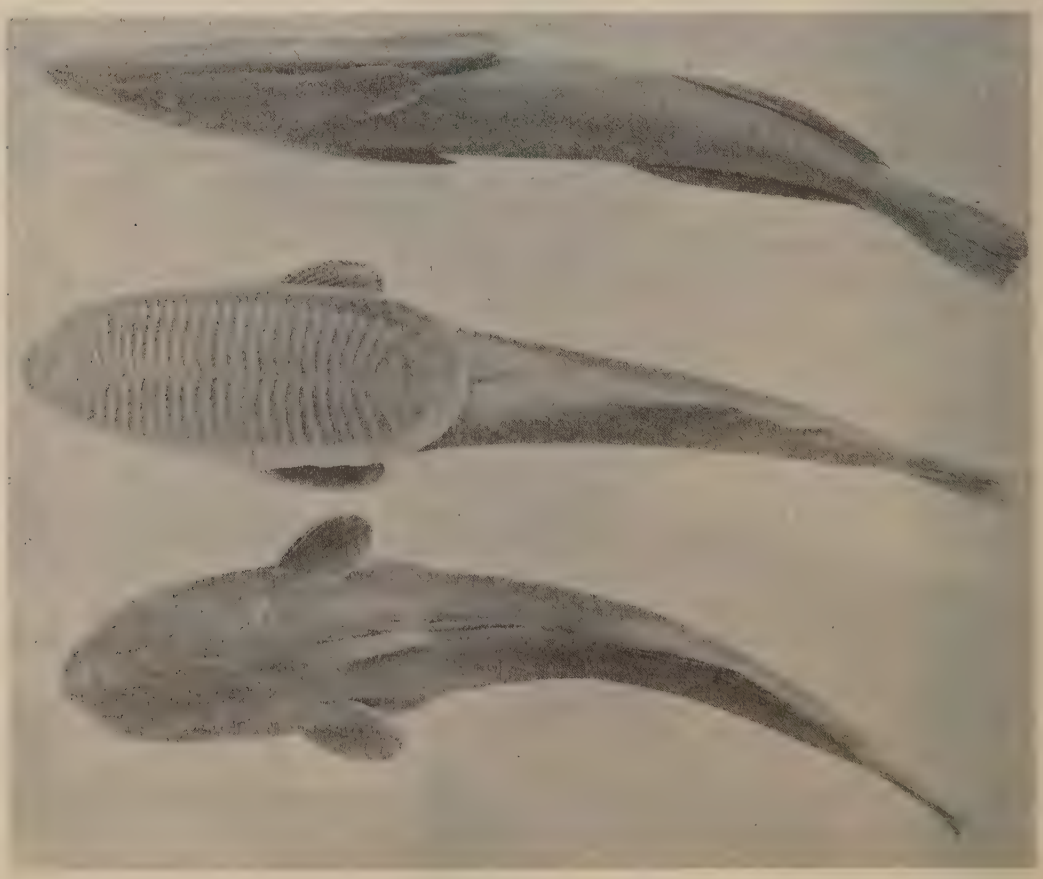

Figure 1. Whalesuckers Remilegia australis. Top: lateral view of a specimen 136 mm. in standard length; middle: dorsal view of a specimen 126 mm. in length; bottom: ventral view of a specimen 122 mm. in length.

the difference in action between a live, swimming whale and a dead whale under tow somehow stimulated the remoras to desert their host. Or possibly the «green» neritic waters through which the vessel passed were repellent to them. All known hosts of the whalesucker inhabit the clear blue water of the deep oceanic zone. Another possibility is that the vibration of the vessel's engine or propellor was repellent to them.

In the water, the remoras changed position on the dead whale by propelling themselves with the tail and sliding the sucker over the surface of the whale's body. The pectoral fins, normally, held tightly against the body, were spread during this maneuver. While shifting position, remoras never broke contact with the whale. Contrary to the opinion of Krefft (1953), they do not leave a scar as do Pacific lampreys *(Lampetra tridentata* Gairdner, 1836) (Pike, 1951; Nemoto, 1955) and sea lampreys *(Petromyzon marinus* Linn. 1758) (van Utrecht, 1959).

Whalesuckers are weak swimmers, and appear highly vulnerable to predation when not attached to cetaceans.

In the whaling stations, all the remoras were alive and in good condition when found, despite having been out of the water, in one instance, for three hours. They were inactive while attached to the whales. They wriggled energetically when captured and handled. They readily clung to the back of a man's hand when their sucker was applied to it.

Color.

The living whalesuckers were dark slate gray. Follett and Dempster (1960) summarized the color variations as reported in the literature.

Captain Newton claims they turn darker when on the dorsal surface of a whale, and lighter when on the ventral surface. We have not observed color changes. Remoras on the pure white ventral portions of a sei whale were as dark as those clinging to the gray dorsal surface.

Food Habits.

The stomach of the largest (399 mm. in standard length) specimen contained bits of chitinous material, probably remains of crustaceans. The remains were too large and thick to be from the euphausiids on which the whale had been feeding. Bits of sloughed-off whale epidermis (?) were also present. The stomach of a 222-mm. individual contained large sections of an almost papery material. Examined microscopically, it also appeared to be epidermal tissue.

The stomachs of 15 specimens (105 to 380 mm. in standard length) were empty. These 17 individuals are all of those reported by Follett and Dempster (1960), with the exception of the Scripps Institution of Oceanography specimen.

Acknowledgements.

John and Charles Caito of the Del Monte Whaling Station, and Robert Casebeer of the Golden Gate Whaling Station, both of Richmond, California, kindly placed at our disposal the facilities of their respective stations. Gilbert Hunter, Loyd Newton, Harold Ridle, and Grant Yost supplied details of their observations aboard whaling vessels. W. I. Follett and Lillian J. Dempster graciously permitted us to examine the California Academy of Sciences' specimens for stomach contents. Victor B. Scheffer assisted in the microscopic examination of stomach contents, and read the manuscript. Melba C. Caldwell and Karl W. Kenyon made a number of helpful criticism of the manuscript.

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SYMPOSIUM ON IMMUNOGENETIC CONCEPTS IN MARINE POPULATION RESEARCH

Special Immunological Techniques for the Study of Marine Populations

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Special immunological techniques for the study of marine populations may be required because of the nature of the problems one encounters in working with these organisms. Among these problems are the conditions under which blood samples must be taken and studied, the relative unavailability of animals for continuous study, and the small size of the animals at stages when they contribute to important problems (for example, the identification of eggs and larvae of marine fishes). The special techniques which will be discussed were not developed with marine population problems specifically in mind, but they may have important application to these problems. These techniques are special from the standpoint that they are either relatively new or have not been applied extensively.

Important modern techniques for the study of soluble antigens are those of immunodiffusion. The single diffusion method of Oudin, which is conducted by allowing an antigen solution to diffuse into a semisolid medium containing an antiserum, results in the formation of bands of precipitation. Since the formation of these bands is dependent upon the diffusion rate of each antigen and the relative concentration of the antigens and their specific antibodies, separate bands may be formed for each antigen antibody system. This method is especially useful for determining the number of antigenic components in a mixture or the number of antibodies in an antiserum. Possible modifications and applications of this method will be discussed.

The Ouchterlony method of double-diffusion precipitation analysis allows both antigens and antibodies to diffuse toward each other through a thin layer of semisolid agar medium. This method results in the formation of lines of precipitate at the position in the medium where an antigen meets its specific antibody in optimal portions. Since the position of the lines is dependent upon the diffusion rates of the antigen and antibody, and on their relative concentrations, separate lines may be formed for each antigen and antibody system. The chief advantage of this method is that it allows side-by-side comparisons of antigenic mixtures or of antisera so that the qualitative identity or relationships of their components may be determined directly. Possible modifications of this method and its application to marine population problems will be discussed.

Among the methods available for the study of differences in cellular antigens worthy of more extensive application to problems of marine populations is the use of fish as the antibody producer. As Landsteiner pointed out, animals for the production of antibodies should be closely related to the animal under study, in order to take advantage of their better "immunological perspective." Especially important is isoimmunization, or the use of another member of the same species for the production of blood-group antibodies. Studies on isoimmunization of fishes and the use of fish as antibody producers will be discussed.

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BLOOD TYPES IN PACIFIC SALMON

by

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ABSTRACT

Intraspecific differences in erythrocyte antigens (blood types) were shown to occur in four species of Pacific salmon, the sockeye or red salmon (*Oncorhynchus nerka*), the chinook or king salmon (*O. tshawytscha*), the chum salmon (*O. keta*), and the pink salmon (*O. gorbuscha*). Antisalmon-erythrocyte sera prepared in rabbits and chickens were used after absorption of species-specific antibodies. Some of these blood types were shown to differ in their frequency of occurrence between different geographic races. In addition, isoimmunizations were conducted on one race of sockeye salmon. Antisera of seven different specificities were prepared and at least eight different patterns of antigenic composition were displayed by the cells tested.

These results indicate that considerable antigenic diversity exists in salmon. Reagents to detect valuable markers for the investigation of geographic races of salmon should be obtained through further research.

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INTRODUCTION

One of the most important problems in fishery biology is recognition of " races ", or reproductively isolated subpopulations, of fishes. Since there may be little or no interbreeding or recruitment between such populations, successful regulation or management of fishery resources must be conducted in such a way as to recognize their independence.

Present methods for distinguishing between the races of a particular species of fish are based on tagging by various means, or by searching for morphometric or meristic differences between the races (Rounsefell and Everhart, 1953).

It has been shown with many animals (Mayr, 1942; Dobzhansky, 1951), including fishes (Gordon, 1947), that reproductively isolated subpopulations of species differ in the frequencies of one of more variable genes. Therefore, a very useful adjunct to the methods of racial identification now used in fishery management and research would be the recognition and definition of genetically controlled polymorphic characters. One class of such characters which has been found in every animal adequately investigated is intraspecific antigenic variations in the red blood cells. These characters are more simply known as blood types.

Landsteiner (1900) was the first to demonstrate the occurrence of blood types. He found them in man with natural isoagglutinins. In the same year, Ehrlich and Morgenroth (1900) demonstrated blood types in goats, using immune isohemolysins induced by transfusions. Subsequently, many additional instances of intraspecific antigenic differences have been demonstrated. The results are most notable in the case of man (Race and Sanger, 1954), cattle (Stormont *et al.*, 1951) and chickens (Briles *et al.*, 1950).

In each of these species, blood types have been used to study reproductively isolated populations. Thus, blood type frequencies have been used to characterize races of men (Boyd, 1950; Mourant, 1954), breeds of cattle (Owen *et al.*, 1947) and inbred lines of chickens (Schultz and Briles, 1953).

The studies of Fujino (1958) demonstrating the occurrence of blood types in whales are of particular interest to marine biologists.

Until recently there have been relatively few published studies concerning the possible existence of blood types in fishes. Some of these demonstrated marked interspecific differences in cellular antigens but provided little or no evidence for intraspecific heterogeneity of such antigens. Noguchi (1903 a, b) found that the serum of several species of fishes would agglutinate the red blood cells of other species but no

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intraspecific differences were noted. He did produce isoagglutinins and isohemolysins in two species of turtle, *Chrysemys picta* and *Chelopus guttatus*, demonstrating that cold-blooded vertebrates may possess intraspecific antigenic differences. Toth (1932) found no evidence for the existence of blood types in carp from 280 crossmatches. Jensen (1937) tested for natural isoagglutinins in the cod (*Gadus morhua*) and also attempted to demonstrate individual differences with the serum of a single rabbit immunized with the red cells of an individual cod. He did not find any conclusive evidence for the existence of blood groups in cod.

Suyehiro (1949) reviewed the previous Japanese literature, in which there were no instances of the demonstration of blood types in fishes. He was evidently the first to demonstrate individual antigenic differences in fish blood cells, since he found a few instances of natural isoagglutinins in the eel (*Anguilla japonica*) and the gilthead (*Sparus swinhonis* (Günther)). In 249 crossmatches of blood cells and serum from cod (*Gadus macrocephalus*), he found no evidence for natural isoagglutinins. Suyehiro (1949) also tested blood samples from 336 fishes of 30 different species with human ABO blood typing sera and found that only 91 were agglutinated. In 21 of the 30 species, individuals varied in their reactivity to the human sera tested.

Cushing and Sprague (1953) studied the agglutinative activity of human anti-A and anti-B sera and rabbit antisheep cell serum for the erythrocytes of a number of species of fish. Considerable antigenic diversity was noted between species but no individual differences were found within the members of the species tested.

Recent reports have indicated a major breakthrough in the efforts to discover blood types in fishes. Hildemann (1956) applied the method of isoimmunization, which has been so successful in detecting blood types in other animals, to goldfish (*Carassius auratus*). One of the isoimmune sera detected six different antigenic types of goldfish. Immune rabbit sera were also prepared by Hildemann, one of which detected a single antigenic difference after careful absorption. Cushing (1956) reported the existence of individual antigenic differences in the oceanic skipjack (*Katsuwonus pelamis* (Linnaeus)) detectable with natural isoagglutinins, normal bovine serum, and the sera of rabbits immunized with the whole blood of oceanic skipjack, albacore (*Germo alalunga* (Gmelin)), or Pacific mackerel (*Pneumatophorus japonicus diego* (Ayres)). Cushing and Durall (1957) discovered and analyzed a natural isoagglutinin system in the brown bullhead (*Ictalurus n. nebulosus* (LeSueur)). This system was found to be analogous to the human ABO system in that four antigenic types were found (i.e., some fish possessed antigen 1, some antigen 2, some both antigens, and some had neither), and when an antigen was lacking, its corresponding isoagglutinin was always present. Ridgway, Cushing and Durall (1958) found quantitative differences in the reactivity of the cells of individual sockeye salmon (*Oncorhynchus nerka* (Walbaum)) with natural antibodies from pig sera and demonstrated that there were significant differences between geographically separated populations in the frequency of the different types detected.

Suzuki *et al.* (1958) has demonstrated the existence of blood groups in species of tunas and has presented evidence which suggests that differences exist between the blood type frequencies of albacore from the Pacific and Indian Oceans.

The present report provides further evidence for the existence of blood types in Pacific salmons and additional evidence that some of these characters differ in their frequency of occurrence in different races of the same species.

MATERIALS AND METHODS

Most blood samples were taken in the field by severing the caudal artery with a sharp knife and collecting the spurting blood in sterile bottles. Some of the samples, including those used in isoimmunizations, were taken by cardiac puncture. The clotted samples were maintained on ice or in a refrigerator until used. Samples excessively hemolysed or over ten days old were not used for testing. Blood cells from samples as old as three weeks were used for animal inoculation. Cells for testing were washed three times in 10 to 50 volumes of modified Alsever's solution (Bukantz *et al.*, 1946) and adjusted to a 2 per cent concentration in this solution. The use of Alsever's solution as a suspending medium was found to be essential, since salmon red blood cells lysed in saline or phosphate-buffered saline solutions.

Most antisera were prepared by giving intravenous or intraperitoneal injections of 0.5 cc. of a 50 per cent suspension of washed cells. Such injections were given to rabbits and salmon three times a week for three weeks and to chickens every three days for three or four injections. Four to twelve days after the last injection the animal was bled and serum collected. In most cases, in order to detect individual differences, several additional stimulations at intervals of two weeks to a month were required. Some rabbits also received subcutaneous inoculations of washed suspensions of particulate material from lysed red cells in

Freund's adjuvant. The sera were preserved by freezing and stored at −30°C. Serum dilutions were made with phosphate-buffered saline or 1 per cent saline solutions.

Absorptions were performed by mixing a 1/2, 1/5 or 1/10 dilution of the heat-inactivated antiserum with an equal volume of washed packed cells, incubating for one hour at room temperature or in the refrigerator, centrifuging the cells down and decanting the absorbed serum. Usually more than one absorption was required to remove all of the antibody present which would react with the absorbing cells.

Tests were performed by mixing 0.1 ml. of absorbed serum, diluted if necessary, with 0.1 ml. of 2 per cent cell suspension in Alsever's solution in 10×75 mm. tubes. Dilutions are expressed as the final dilution of the original serum, taking into account the dilution by the red cell suspensions. Readings were made after suitable incubation periods at room temperature and usually after overnight incubation in the cold. The settling pattern was judged either smooth (S) or rough (R) and the degree of agglutination scored as 0, ±, 1 plus, 2 plus, 3 plus and 4 plus. In order for a test to be considered, the saline control had to be smooth and negative.

RESULTS

The major part of our effort has been directed toward finding blood types in red or sockeye salmon (*Oncorhynchus nerka* (Walbaum)). Toward this end, we have immunized 26 rabbits and 20 chickens with the washed erythrocytes or stroma from members of this species. For each of the other species of Pacific salmon we have made 2–8 rabbit and chicken antierythrocyte sera. Individuals or pools from individuals from the same area were used. These antisera were absorbed with the erythrocytes of individual salmon from other areas and the resulting sera tested for residual activity for the cells of a number of individuals. With most antisera produced, numerous absorptions did not reveal any evidence for antigenic heterogeneity within this species. However, blood group differences were demonstrated with a few rabbit immune sera. One of these sera (R 19) was analyzed by absorption with the cells of sockeye salmon collected in 1955 from Cultus Lake and the Adams River, both tributary areas on the Fraser River in British Columbia (Table 1). The three samples tested from the Adams River race removed all or nearly all of the antibodies present in the serum. The three samples from the Cultus Lake race each removed all of the antibodies specific for their antigens, but left antibodies which would react with antigens present on the cells of other individuals tested. Thus, three reagents of different specificities were produced.

These results, as well as additional tests made on samples collected from these areas in 1956 with the above absorbed sera, are combined in Table 2. Statistically significant differences in the proportion

TABLE 1. Individual antigenic differences demonstrated by agglutinin absorption tests in the erythrocytes of sockeye salmon from Cultus Lake and Adams River. (Rabbit antisockeye salmon-erythrocyte serum R19 absorbed and cross-tested with the cells of individual salmon.)

Absorbing cells	Test cells									
	Cultus Lake					Adams River				
	1	15	19	12	13	15	11	9	13	8
Cultus Lake 1	0	+	0	+	0	+	+	+	+	+
Cultus Lake 15	+	0	+	+	+	+	+	+	+	+
Cultus Lake 19	+	+	0	+	0	+	+	+	+	+
Adams River 15	0	0	0	+	0	0	0	0	+	0
Adams River 11	0	0	0	0	0	0	0	0	0	0
Adams River 9	0	0	0	+	0	0	0	0	0	0
Adams River 13	0	0	0	0	0	0	0	0	0	0
Saline control	0	0	0	0	0	0	0	0	0	0

TABLE 2. Serological differences between races of Fraser River sockeye salmon.

Area (test cells)	Number tested	Number reacting with reagents prepared by absorbing rabbit R19 serum with cells of			Number not reacting with any of the three reagents
		Cultus Lake 19	Cultus Lake 1	Cultus Lake 15	
Cultus Lake	17	3	2	12	4
Adams River	17	11	17	16	0
Chi-square		7.6*	56.6*	3.3	4.5*

* Significantly different at the 95 per cent level.

of individuals reacting positively with these reagents are apparent for the two populations.

Some of the antisalmon red blood cell sera, prepared in rabbits and chickens, were useful in demonstrating blood group differences in species of salmon other than the one used for immunization. This is somewhat analogous to the demonstration of the Rh blood groups in humans by Landsteiner and Wiener (1941), through the use of anti-Rhesus monkey red blood cell sera.

The evidence for blood groups in chinook or king salmon (*O. tshawytscha*) is presented in Table 3. Absorption of serum R 13, an antisockeye salmon red blood cell serum, by the cells of four different chinook salmon from the Columbia River, resulted in the production of reagents of four different specificities. The results indicate a characteristic present in number one which is absent from the other three. Superimposed on this, there appears to be a kind of subtype difference between 2, 3 and 4, which is shared with 1.

Evidence for blood groups in chum salmon (*O. keta*) is presented in Tables 4 and 5. The experiments outlined in these tables were performed with samples from the Samish River in Washington State. Evidence for the presence of a considerable amount of antigenic heterogeneity in this species and this race is provided by the results presented in Table 4, since reagents of four different specificities were obtained by five different absorptions.

Five patterns of reactivity were displayed by the samples tested; numbers 1, 6, 8 and 9 reacted with the sera absorbed by 2, 4 and 5; numbers 2 and 7

TABLE 3. Demonstration of individual antigenic differences in chinook salmon erythrocytes using rabbit antisockeye salmon serum. (Serum R13 absorbed and cross-tested with four individual samples of chinook erythrocytes.)

Absorbing cell sample numbers	Test cell sample numbers	Dilutions of absorbed sera			
		1 : 10	1 : 20	1 : 40	1 : 80
1 (a)	1	0	0	0	0
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0
2	1	++++	0	0	0
	2	±	0	0	0
	3	0	0	0	0
	4	0	0	0	0
3	1	++++	++	0	0
	2	+	±	0	0
	3	0	0	0	0
	4	0	0	0	0
4 (b)	1	++++	++++	+++	+
	2	++++	+++	0	0
	3	++++	+++	++	0
	4	+	0	0	0

(a) This absorbed serum tested against the cells of an additional 12 chinook salmon, none of which reacted. Positive reactions were obtained with the cells of 12 different sockeye salmon.

(b) This absorbed serum tested against the cells of 24 additional chinook salmon. Definite reactions occurred with 16 of them.

TABLE 4. Demonstration of blood types in chum salmon using chicken antichinook salmon serum. (Serum 202 absorbed and tested with cells of individual chum salmon.)

Absorbing cell sample numbers	Test cell sample numbers								
	1	2	3	4	5	6	7	8	9
1	0	+	+	++	0	0	+	0	0
2	++	0	++	0	++++	++	0	++++	++
3	0	0	0	+	0	0	0	0	0
4	+++	0	++	0	+++	++	0	+++	+++
5	+++	++++	++	++++		++	+++	+	+
7	0	0	0	0	0	0	0	0	0

TABLE 5. Demonstration of blood types in chum salmon using chicken antisockeye salmon sera.

Sera	Test cell sample number													
	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Serum 210:														
Absorbing cell														
No. 18	+	++++	+++	++	++++	++++	++++	0	+++	+	+++	+++	++++	+++
No. 20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. 23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. 24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serum 220:														
Absorbing cell														
No. 18	++	++++	++	++	++++	+++	+++	0	++	+	++	++++	+++	++
No. 20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. 23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. 24	0	0	0	0	0	0	0	0	0	0	0	0	0	0

reacted with the sera resulting from absorption by 1 and 5; number 4 reacted with the sera resulting from absorption with 1, 3 and 5; number 3 reacted with sera from absorption with numbers 1, 2, 4 and 5; and number 5 reacted with the sera from absorption with numbers 2 and 4. The results obtained with individuals 2, 4 and 7 demonstrate some of the complexities involved in the antigenic differences between individuals of a single species. All gave the same reaction with the reagents prepared, except for the weak reaction of the cells of individual 4 with the reagent prepared by absorption with the cells of individual 3. Consistent with this is the fact that reagents of identical specificity were prepared by absorption with cells of individuals 2 and 4. In contrast, absorption by cells of individual 7 removed the antibodies reactive with the cells of all individuals tested, but the cells of individual 7 failed to react detectably in agglutination tests with reagents prepared by absorption with cells of individuals 2, 3 or 4. Such apparent deviations from the principles upon which absorption analyses are generally assumed to rest have been associated, in other species, with the multiple-allelic control of sets of related but nonidentical specificities. The large amounts of cells required to absorb the antibodies present in this serum which would agglutinate the cells of all members of the species, precluded further investigation of this system.

The results presented in Table 5 are less complicated with apparently a single difference detected between chum salmon sample 18 and the others tested. Superimposed on this, however, are rather marked differences in the strength of reactivity of the other cells tested which may indicate additional antigenic heterogeneity.

Evidence for the existence of blood group differences in pink salmon (*O. gorbuscha*) is presented in Table 6. A single difference was noted which appeared to be correlated with the area of origin of the samples tested. However, positive statements about area differences must await analysis of a larger number of samples.

In addition to rabbit and chicken immunizations, extensive isoimmunizations have been conducted on sockeye salmon (*O. nerka*). The fish used in all of these experiments were from the Columbia River (where this species is known as the blueback salmon). In 1955 and 1956, 20 to 30 adult salmon migrating up the Columbia River were captured and isoimmunized over periods of one to two months without any detectable development of isoimmune antibodies. Since many of these fish died before an adequate period for the production of isoimmune antibodies had elapsed, no conclusions about the antigenic heterogeneity of salmon could be drawn from these experiments.

In order to have fish available for isoimmunization over a longer period, a group of sockeye yearlings were obtained from the Winthrop Hatchery of the United States Fish and Wildlife Service in 1956, and reared in salt water at the Deception Pass Marine Research Station of the State of Washington Department of Fisheries. Isoimmunizations involving 100 fish, 50

TABLE 6. Demonstration of blood groups in pink salmon. (Antiserum chicken E213 absorbed with red blood cells from Cordova pink salmon #6.)

	Sashin Creek							Kodiak					Cordova
Sample number	1	2	3	4	5	6	7	1	3	4	5	9	6
Reaction	–	–	–	–	+	–		+	+	+	+	+	–

pairs being cross-immunized, were started in August of 1957. During the period of this experiment the water temperature ranged from 14°C. to 9°C. with a mean of approximately 12°C.

Of these 100 fish, 15 produced isoimmune antibodies after periods of 7 to 14 weeks and 5 to 11 inoculations. Because of the small size of these salmon, due to their being reared in captivity, only small amounts of the isoimmune sera could be collected. In addition, the sera were of low titer, most reacting only to 1 in 4 dilution. Sufficient amounts of serum were obtained from seven of these fish to compare the specificity of the reactions against a number of individuals.

The results of these tests are presented in Table 7. Inspection of these data reveals that all seven of the sera possessed different patterns of specificity, and at least eight different patterns of antigenic composition were shown by the cells tested. Thus, it would appear that the extent of antigenic variability in salmon is of the same order of magnitude as that found in other animals which have been extensively studied. Further study and application of this heterogeneity will depend on the availability of larger salmon, and experimental facilities for holding them.

TABLE 7. Comparison of the specificities of isoimmune sera produced in sockeye salmon.

Cells	Serum						
	14-4	14-6	14-10	15-1	22-10	24-2	13-2
13-1	0	0	+	+	+	+	+
14-3	+	0	0	0	0	+	0
14-5	0	+	0	+	0	0	0
14-9	0	0	+	+	0	+	0
15-1	—	+	+	0	—	0	0
15-7	0	0	0	—	—	—	0
22-9	—	—	—	—	+	+	0
22-10	+	+	0	+	0	—	—
24-1	+	+	0	+	—	+	0

+ Agglutination, 0 No agglutination, — Not tested.

DISCUSSION

The demonstration of blood group differences in four species of Pacific salmon, as outlined in this paper, along with the demonstration that, in some cases, these characters can serve as markers of racial identity, indicates the existence of valuable tools for the solution of many of the population problems encountered in the management and conservation of these important fishes. However, more research and developmental work must be done. One of the biggest problems is in the production of sufficient type-specific sera to test large numbers of individuals from populations of interest. In all of the immune sera we have produced in rabbits and chickens, most of the antibodies reacted with antigens possessed by all members of the species or genus. The production of type-specific sera in even small amounts required large quantities of cells for absorption.

It is interesting to note that several of the immune sera were capable of demonstrating blood group differences in a species other than the one used for immunization, but could not be used to demonstrate differences in the immunizing species. This would appear to indicate that related antigens are fixed in one species and segregating in another. These observations are somewhat analogous to antigenic relationships which have been demonstrated between man and Rhesus monkeys (Landsteiner and Wiener, 1941), and recently between cattle and bison (Owen, Stormont and Irwin, 1958), and between tahrs (*Hemitragus jamlahicus*) and a variety of other Artiodactyl species (Stormont and Suzuki, 1958). Further extension of these observations in fishes may result in the production of type-specific sera in practical quantities.

Our isoimmunization experiments with sockeye salmon indicate considerable antigenic diversity exists in this species. Similar and more extensive studies have been conducted with rainbow trout and will be presented in another paper. As with other animals, isoimmunization appears to be the most promising approach to the problem of blood group differences in fishes. The species of Pacific salmon are particularly difficult animals on which to conduct isoimmunizations, as they invariably die after becoming sexually mature at two to six or seven years of age. It is only shortly before their death (two weeks to three or four months), while they are on their spawning migration, that they become readily available. They also grow quite slowly in captivity and only one species, the sockeye, can be readily held in fresh water throughout its lifetime. At least some of these difficulties can be overcome and we hope to continue our attempts to do so.

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SUMMARY

1. Through the use of absorbed rabbit and chicken antisalmon-erythrocyte sera, blood types were demonstrated to occur in sockeye, chinook, chum and pink salmon.
2. Some of these types appear to differ in their frequency of occurrence between different geographic races.
3. Isoimmunizations between individuals of the race of sockeye salmon indicated the existence of at least eight different antigenic types or combinations of types within this race.
4. The usefulness of this kind of research to fishery management and some of the problems involved in its practical utilization are discussed.

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SEROLOGICAL DIFFERENTIATION OF POPULATIONS OF SOCKEYE SALMON, *ONCORHYNCHUS NERKA*

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ABSTRACT

As part of a study applying serological methods to the distinction of salmon races, the normal serums of human beings, cattle, horses, sheep, pigs, goats, brown bullheads, and other salmon were tested for agglutinative activity with the erythrocytes of sockeye salmon. Only horse serum and pig serum reacted strongly with the salmon cells. With some of the pig serums tested, consistent differences were found in the strength of reaction of the cells of individual sockeye salmon. The frequencies of individuals displaying the various strengths of reaction were found to differ significantly between areas of origin of the salmon tested. When techniques of population genetics were used, evidence for the possible genetic control of the observed differences was obtained.

INTRODUCTION

This is a report on the results of a collaborative investigation[1] of the differentiation of sockeye salmon (*Oncorhynchus nerka* Walbaum) populations by serological methods. The aim of the work was to estimate the potential value of agglutinins found in the nonimmune serums of animals (so-called " natural antibodies ") for detecting racial variations among salmon erythrocyte antigens. Such agglutinins have been used successfully in research on the erythrocyte antigens of man, cattle, sheep, chickens, and other warm-blooded animals. (Cf. Cushing and Campbell, 1957, for a general account of these reactions). They have also been used to demonstrate individual variations in the erythrocyte antigens of skipjack, *Katsuwonis pelamis* Linnaeus (Cushing, 1956) and brown bullheads, *Ictalurus n. nebulosus* Le Sueur (Cushing and Durall, 1957), and other fishes (Suyehiro, 1949).

Variations in erythrocyte antigens provide favorable material for racial analyses, since whenever studied their genetic determination has been found to be simple and direct. Also their specificity has not been found to be subject to environmental influences. Evidence for the genetic determination of such variations in fish has recently been provided by Hildeman (1956), and the potential utilization of these antigens in fishery research has been discussed by Cushing and Sprague (1953), and by Ridgway (1957).

MATERIALS AND METHODS

Samples of whole salmon blood were obtained by field crews from the major salmon-producing rivers of North America and were either shipped immediately by commercial air transport or brought directly to the laboratory. These samples were collected by bleeding salmon from the tail into open-mouth screw-cap bottles without preservative or anticoagulant. The largest collections were made in the rivers of Bristol Bay and at various localities in the Columbia River System. The clotted bloods (approximately 5 to 50 ml.) were transported in bottles in insulated picnic jugs containing ice. They were usually received from 1 to 3 days after collection and were kept refrigerated at 5 to 10°C. until used. Under these conditions most of the samples remained useful for a week or two.

Suspensions (1.5 per cent) of fresh cells were prepared on the day of use by washing 1.5 ml.

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aliquots of whole blood in three 20 ml. changes of Alsever's solution. All washings were carried out in a refrigerated centrifuge, and the cell suspensions were kept refrigerated except when in immediate use. Individiual tests were performed by placing two drops of suspension with two drops of suitable serum dilution in 10 × 70 mm. test tubes. After 15 minutes incubation at room temperature, the tubes were centrifuged for 1 minute. The sedimented cells were resuspended by lightly tapping the tube and the degree of agglutination was scored in the conventional manner (4 indicating very strong, 3 strong, 2 moderate, 1 light and ± barely detectable agglutination with 0 indicating no agglutination).

The influence of variables such as the speed of centrifuging, age of cells, temperature, etc., were considered and controlled. Efforts were made to control the objectivity and accuracy of the method by testing the same sample on different days and making the readings without knowledge of the sample sources. Readings were also made on the same material by independent observers. Such controls substantiated the comparisons of different tests, provided a basis for evaluating the limits of experimental error in these tests, and suggested refinements in technique for control of such error.

EXPERIMENTAL RESULTS AND DISCUSSION

Several serums from humans,[2] cattle, horses, sheep, pigs, goats and fish, all preserved by freezing, were titrated against sockeye cells. Included were a number of cross matches (approximately 700) of cells and serums (1 in 4) between sockeye samples from various localities. All of the latter gave negative results, an observation that is in contrast to those that have been made on the brown bullhead, the white croaker (*Genyonemus lineatus* (Ayres)) and skipjack (Cushing and Durall, 1957). Some brown bullhead serums (6 out of 16) were found to react strongly with sockeye cells at 1 in 4 dilution. However, these serums did not differentiate among sockeye from different areas. There also appeared to be no relation between the positive reactions and the blood group of the brown bullhead involved.

It is of interest that bovine serum which proved so useful in detecting individual differences in chickens and in skipjack reacted very poorly with sockeye cells.

Pig and horse serums were found to agglutinate sockeye cells more strongly than the other serums examined. As titrations of several single pig serums with the cells of different fish showed differences in the strength of reactions with these cells, attention was concentrated on this observation. While the optimum temperature of agglutination for this serum was approximately four degrees, it was practical to work only at room temperatures which consistently remained at 22° to 24°C.

A standardized procedure was adopted for the comparison of readings of different sets of samples. This procedure consisted of testing the cells of each fish against four dilutions (1 : 16, 1:32, 1:64 and 1:128) of heat-inactivated (56°C. for 30 minutes) serum from a single pig designated W.P.4. The scores of the readings at the latter three dilutions were added to give a single total score. Table 1 presents an example of the protocol just described. Figure 1 presents a summary of scores from many such protocols, which combines the samples into three groups. The first of these consists of samples taken from the rivers of Bristol Bay, the second of samples taken from rivers of the eastern Pacific coast from Kodiak Island to the Fraser River, the third of samples taken in the Columbia River System. An analysis of variance was performed (Table 2), which shows that the three groups differ significantly. This analysis was performed by the method given in Snedecor, 1957, page 283, which takes into account the differences in variances. This is the first time that it has been possible to demonstrate a statistically significant serological difference between populations of individuals within a single species of fish.

It should be borne in mind that the salmon in each of these areas are homing toward a variety of separate and distinct spawning grounds. In spite of this it seems reasonable that genetic exchanges may be more frequent within the Columbia and Bristol Bay groups than between them, and that this would plausibly account for the differences observed.

Consideration of all the individual scores of the above groups suggests that these form a trimodal distribution (Figure 1). Some statistical justification for the validity of this suggestion was obtained by applying a test for bitangentiality (Haldane, 1952).

Additional evidence of antigenic heterogeneity was obtained from absorption experiments. Samples of the serums of several pigs were absorbed with strong and weakly reactive cells. In general, two capacities for antibody removal were observed. Several absorptions indicated that weaker reacting cells (Bristol Bay) were less

2. Human typing serums kindly supplied by Hyland Laboratories, Los Angeles, California.

TABLE 1. Comparison of the Strength of Agglutination of Bristol Bay and Columbia River Sockeye Salmon Blood Samples by Serum WP4.

Serum Dilutions	Areas																					
	Kvichak (Bristol Bay)												Columbia River									
	Samples												Samples									
	1	2	3	4	5	6	7	8	9	10	11	12	12	13	14	15	16	17	18	19	20	21
1 : 16	2	3	3	3	3	3	4	3	4	3	4	4	4	4	4	4	4	4	4	4	4	3
1 : 32	2	2	2	2	2	1	3	1	2	2	2	2	3	3	3	3	3	3	3	3	3	3
1 : 64	±	±	±	±	±	±	1	±	1	±	1	1	1	2	3	1	2	2	2	2	2	1
1 : 128	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	±	±	±	±	0	0
Score	2.5	2.5	2.5	2.5	2.5	1.5	4	1.5	3	2.5	3	3	4	6	7	4	5.5	5.5	5.5	5.5	5	4

4 indicates very strong, 3 strong, 2 moderate, 1 light and ± barely detectable agglutination. The scores are obtained by adding the readings of the highest three dilutions.

TABLE 2. Frequencies of Agglutination Scores of Sockeye Salmon

Scores	Areas		
	Bristol Bay No. of Fish	Gulf No. of Fish	Columbia No. of Fish
0	1	0	0
0.5	3	0	0
1.0	6	0	0
1.5	2	1	0
2.0	9	2	0
2.5	14	6	3
3.0	14	23	4
3.5	3	4	1
4.0	4	11	7
4.5	1	3	1
5.0	0	7	4
5.5	0	1	7
6.0	0	0	11
6.5	0	0	1
7.0	0	0	3
7.5	0	0	0
8.5	0	0	1

Analysis of Variance

Source of Variation	Degrees of Freedom	Mean Square	F
Between means	2	61.3638	61.32**
Error	96	1.0007	

** Highly significant

effective in removing antibodies than stronger reacting cells (Columbia River).

One exceptional serum was discovered. This serum appeared to have antibodies that were relatively more amenable to fractionation. Absorption of this serum with the cells of a Bristol Bay fish left considerable antibody for the cells of a Columbia River fish while absorption with the cells of the Columbia River fish removed all the antibody for both types. The small amount of this serum that was available prevented a systematic expansion of this observation. However, the occurrence of this serum shows that a study of the serums of other pigs may prove to be profitable.

The discovery that the erythrocytes of salmon from different geographic areas vary significantly with respect to their reactions with antibodies in pig serum raises the question of the nature of the mechanism controlling this variation. While the answer to this question awaits further study, several sources of evidence indicate that a genetic mechanism probably exists. First, the erythrocyte antigens of mammals and birds have been found to be genetically determined wherever investigated. Second, Hildeman (1956) has shown that certain erythrocyte antigens of goldfish have hereditary determinants. Third, different species of salmon (Ridgway and Klontz, 1957), as well as other species of fish (Suyehiro, 1949; Cushing and Sprague, 1953), show characteristic species specificities with respect to their erythrocyte antigens. This suggests that the antigenic specificities involved are genetically determined.

An analysis of the frequency distributions of the antigenic variations in sockeye salmon populations was made with the Hardy-Weinberg formula (Srb and Owen, 1953) in an attempt to obtain further information concerning the possible genetic background for these variations. The Hardy-Weinberg formula relates the frequencies of allelic genotypes to the frequencies of allelic genes in a randomly mating population, in terms of the binomial expansion. It was through the use of this formula that Bernstein determined the exact method of inheritance of the human ABO groups (see Race and Sanger, 1954) and it is an indispensable tool in the study of the population genetics of blood groups in man and animals.

Our interpretation of the data presented is based upon the assumption that the observed variations in strength of agglutination, expressed in terms of high, intermediate and low scores,

TABLE 3. Application of the Hardy-Weinberg Formula

Populations	Total Number of Fish N	Categories						"Gene" Frequencies	
		aa		aA		AA			
		Observed	Expected (p^2N)	Observed	Expected ($2pqN$)	Observed	Expected (q^2N)	p	q
Bristol Bay	57	49	49	8	7	0	<1	0.43	0.07
"Gulf"	58	32	29	18	24	8	1	0.71	0.29
Columbia R. Mainstream	43	7	3	9	17	27	23	0.27	0.73
Okanogan	43	5	5	18	19	20	19	0.33	0.67
Lk. Wenatchee	64	4	2	16	19	44	42	0.19	0.81
Composite "Population"	265	97	65	69	133	99	67	0.496	0.504

$$p=\frac{2(aa)+(aA)}{2N} \qquad q=\frac{2(AA)+(aA)}{2N}$$

The frequencies of weak (aa), intermediate (aA), and strong (AA) reactors observed in the various populations of sockeye salmon are compared with those expected on the basis of the Hardy-Weinberg Law.

are due to two primary causes.

The first is that the active agglutinin in serum WP4 has a lower affinity for a qualitatively different but related antigen on the surface of the lower scoring cells than for the antigen on the higher scoring cells. Since our absorption results indicate that these antigens must be serologically related, because they react with the same agglutinin, we assume that they are determined by allelic genes. Differences in the strength of agglutination brought about by the reaction of one type of antibody with different antigens determined by allelic genes are well documented in the literature on blood groups (Race and Sanger, 1954).

The second primary cause of variation must be postulated to account for the intermediate reactions. This is assumed to be a dosage effect causing a stronger reaction with cells of individuals homozygous for a particular gene than those of individuals heterozygous for this gene. Dosage effects exhibited by blood grouping reagents are also well documented in the literature; in fact, the scoring system used by Race, Sanger and Lehane (1953) in their study of the dosage effect in the human Duffy blood groups serves as a model for our scoring system.

The apparent trimodality of the distribution of agglutination scores (Figure 1) served as a basis for assigning individual fish to one of three categories, rated as strong, intermediate and weak reactors. These categories, as explained above, may be postulated to correspond to three genotypes determined by a single gene and its allelic alternates. Strong reactors are considered as homozygous for this gene (symbolized AA), intermediate reactors as heterozygous (Aa) and weak reactors as lacking this gene (aa). The numbers of fish occurring in each category are compared with those expected on the basis of the Hardy-Weinberg formula in Table 3.

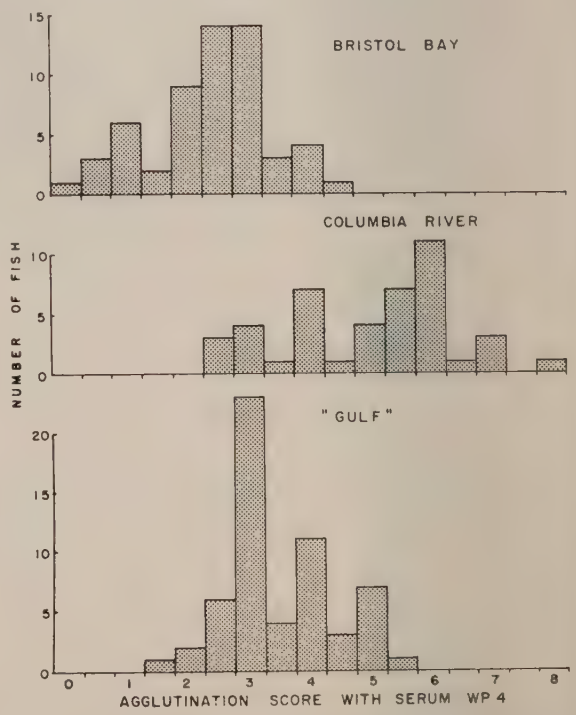

FIGURE 1. Histograms showing the agglutination strengths of sockeye salmon erythrocyte samples from three populations.

Two groups of fish drawn from spawning populations were also studied. These were taken

from the Okanogan River and the Little Wenatchee River which are the major spawning areas for Columbia River sockeye salmon. Since these two populations were examined at a later date and under somewhat different conditions, it is necessary to assign the individual fish to the three categories on the basis of the modes present in the population, rather than according to standard score values. For this reason, the present analysis must only be considered as a guide toward further studies under more refined conditions.

It is of interest that the Mendelian populations taken from spawning grounds gave data that appear to fit the Hardy-Weinberg equation quite well, while two out of three populations that were known to be mixtures of breeding stocks did not, nor did a composite of all populations (Table 3). In the two cases where the number of fish was sufficient in all categories for the application of the Chi Square test these conclusions appear to be statistically sound. (Okanogan River $\chi^2=0.106$ $d.f.=2$, "composite population" $\chi^2=61.9$ $d.f.=2$).

Although the close agreement of the actual Bristol Bay data with the Hardy-Weinberg Law may possibly be due to chance alone, the results may tentatively be ascribed to the several populations in this system being genetically homogeneous with respect to the relative frequencies of "A" and "a". While the reasons for and implications of this homogeneity remain to be determined, three not mutually exclusive possiblities suggest themselves. The first is that the various "parent-stream" stocks, while genetically isolated, have not diverged with respect to the frequencies of these genes as they obtained in a common ancestral stock. The second is that the various "parent-stream" stocks are not sufficiently isolated to allow for divergence of the frequencies of the two alleles among them. The third is that identical selection pressure in the separate populations may impose identical points of genetic equilibrium.

The failure of the Columbia River and Pacific Coast samples to conform to the Hardy-Weinberg formula can be explained by the fact that each represents a mixture of populations differing with respect to the frequencies of A and a. This explanation receives support from consideration of the good fit of samples obtained on the spawning grounds of the upper Columbia after the Wenatchee and Okanogan runs had separated from each other. In these cases, where fairly large samples were taken from known Mendelian populations, the distribution of scores does conform to the Hardy-Weinberg law. In view of these various considerations there seems to be good reason to postulate that the variations in erythrocyte antigens which we are comparing are genetically controlled by a simple allelic system of genes, the frequencies of which may vary in racial stocks of different geographic origins.

ACKNOWLEDGEMENTS

The authors wish to express their sincere appreciation to the faculty of the Department of Microbiology, University of Washington, for making laboratory space available for this investigation; to the many fishery biologists who assisted with the sample collections; to the Biometrics Unit, Pacific Salmon Investigations, for performing the analysis of variance; to Dr. Lucian Sprague for several of the animal serums; and to Mr. G. W. Klontz for technical assistance with some of the experiments.

SUMMARY

1. In over 700 cross matches between the cells and serums of samples from several localities, no evidence was obtained for the existence of natural isoagglutinins in sockeye salmon.

2. The normal serums of several humans, cattle, horses, sheep, pigs, goats and brown bullheads were tested for agglutinative activity with the erythrocytes of sockeye salmon. Only horse serum and pig serum reacted strongly with the salmon cells.

3. Consistent differences were found in the strength of reaction of some pig serums with the cells of individual sockeye salmon.

   The frequencies of the various strengths of reaction, which were expressed as scores, were found to differ significantly between areas of origin of the salmon tested.

4. A hypothesis to explain the possible genetic determination of these differences was presented and tested with the Hardy-Weinberg law.

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ADDENDUM

Since the preparation of this manuscript we have tested somewhat larger samples from Bristol Bay and the Columbia River, taken in the 1957 season, and have repeated the distinction with considerable precision. In 1956, 86 per cent of Bristol Bay sockeye salmon tested had scores less than 3.5 while 83 per cent of those from the Columbia River had scores greater than 3.5. In 1957, 92 per cent of the Bristol Bay fish tested had scores less than 3.5 while 79 per cent of those from the Columbia River had scores greater than 3.5. This year to year stability provides further evidence for the genetic control of the characters determined by this method.

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Longevity of the Horseshoe Crab, *Limulus polyphemus* (L.)

The horseshoe crab, *Limulus polyphemus* (L.), was studied in Plum Island Sound, Massachusetts, and other nearby estuaries that empty into Ipswich Bay. During 1952 to 1954, Petersen disk tags were attached to 1,778 crabs to obtain information about their life history and migratory habits. Since publishing the results of this study (Baptist, Smith, and Ropes, 1957) the authors have received additional tags (Table 1). These recoveries do not alter the general conclusion of the above publication, ". . . that there is a fairly discrete population of horseshoe crabs in Ipswich Bay." The tags recovered to date do, however, provide the longest known record of the longevity of adult horseshoe crabs in their natural habitat (Table 2).

Although only 7.3 percent of the 1,778 tagged horseshoe crabs have been recovered to date, the seven individuals caught 4 to 6 years after release permit an estimate to be made of the adult life span of *Limulus* (Table 2). Shuster (1950, 1954) has estimated that *Limulus* spends 9 to 12 years as an immature individual, molting more than once a year during its early life history and annually after the third or fourth year. Upon reaching sexual maturity, however, adults are believed to cease molting (Shuster, 1950, 1954[1]). Since the molting behavior might permit tags to be retained for the longest period of time on adult crabs, 1,711 of the total number were selected as being adult individuals. The separation of immature from mature individuals required different criteria for each sex. To obtain 848 adult males, we examined the second pair of appendages for the presence of clasping claws which do not appear on immature males. To obtain 863 adult females, we looked for large orange or gray-green ova at the site where a hole was pierced with an awl to insert the tag. Immature females have either small white ova, or none. Although these criteria were useful in separating mature from immature crabs, it was not possible to determine when the crabs had become mature. Most of the crabs had probably matured considerably before tagging since many had hard shells and carried extensive encrustations of organisms such as barnacles and algae. A conservative estimate, therefore, of the adult life span of the individuals caught 4 to 6 years after release would be 5 to 7 years.

These few data do not give conclusive proof of the adult life span of *Limulus*. Although the sharp decrease in tag recoveries following the third year after release could be due to an average adult life span of 3 years, it is more probable that the decrease is due to a loss of tags. Natural mortalities and the deterioration of the pin used in tagging undoubtedly account for some tag loss. Natural mortalities were seen after severe winter storms when large numbers of dead crabs were found washed onto the beaches of Plum Island. The nickel tag pin is subject to corrosion and abrasion as tagged individuals burrow and plow through the sediments in search of food and spawning sites. The loss of tags could, there-

[1] Shuster, C. N., Jr. (1954) On morphometric and serological relationships within the Limulidae, with particular reference to *Limulus polyphemus* (L.). Unpubl. Ph.D. thesis, General University Library, New York University.

TABLE 1.—*Five tag recoveries of* Limulus *during 1957 and 1958*

Release				Recovery		
Date	Sex	Size (millimeters)	Location	Date	Location	Recovered by
August 25, 1952	F	155	Point Peter	June, 1957	Eagle Hill River	N[1]
August 25, 1952	F	157	Point Peter	July 24, 1957	Third Creek	A
August 27, 1952	M	131	Nelsons Island	June 7, 1958	Newbury town wharf	N
June 25, 1954	F	144	Conomo Point, Essex[2]	May 28, 1957	Staceys Creek	A
June 29, 1954	F	157	Point Peter	May 2, 1957	Cape Ann Fisheries, Gloucester[2]	N

[1]N = accidental recoveries by "non-alerted" visitors to the seashore; A = recoveries by "alerted" persons who searched for tagged crabs within Plum Island Sound.
[2]Released or recovered outside of Plum Island Sound.

TABLE 2.—*Total number of tags returned, and years between release and recovery of marked horseshoe crabs*

Years after release	Males	Females	Total
0	9	7	16
1	18	38	56
2	13	15	28
3	9	14	23
4	2	2	4
5	0	2	2
6	1	0	1
Total	52	78	130

fore, be substantial, although the extent of loss is unknown.

In summary, *Limulus* can have an adult life span of 5 to 7 years and, on the basis of estimates of its immature life span, a total life span of 14 to 19 years.

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How Can Research Production Be Measured? [1]

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THOSE RESPONSIBLE FOR THE ADMINISTRATION of research programs find it very difficult to judge whether progress is satisfactory. How can we measure this progress? We must first decide what kind of information should be produced and how this information should be communicated to other research workers, to action levels of administration, to any affected industry, and to the general public.

In answering the question concerning the type of information required, a sharp distinction must be drawn between management and research. A biologist may gather routine data to give management continuous information needed to insure intelligent use of a resource. This is not research. Should these data also prove adequate on analysis to throw new light on some aspect of biology, it would be fair to charge some portion of the cost of collection to research. In many cases, however, an experiment can be designed to bring out the biological facts at less cost, and in more clear-cut fashion, than by using data collected for other purposes. This was well exemplified in Alaska for years before statehood. The problems of management were so great and so pressing that the federal research biologist had to spread his field activities over wide areas and gather data to answer specific questions needed for management in particular localities.

If such a situation were recognized and sufficient funds and personnel made available, perhaps this handicap could be overcome. In the case cited, however, the inevitable siphoning of already inadequate research funds into quasi-research activities delayed the acquisition of basic biological information. In the long run, management suffered from failure to discover some of the underlying biological principles sorely needed for wise management.

Let us then define research as the search for new knowledge. And let us not quibble about basic and applied research. The idea of research for the sake of research and anxiety to avoid the stigma of identification with any organism or process beneficial to man is not a useful concept. There is no dividing line between "basic" and "applied" research. Biological principles may be elucidated through the study of any species whether or not it is currently useful to man.

The second question—communication—has plagued scientists for years.

[1]Contribution No. 133 of the Galveston Biological Laboratory, U.S. Bureau of Commercial Fisheries.

There is often a long gap between the completion of a piece of research and the appearance and dissemination of a technical report. In fact, this is one of the main arguments favoring annual reports of research groups chronicling the progress and stage of completion of each research project.

Following a technical report on a research project there often arises need for translation of the report into a summarized and simplified account of the facts or principles studied, with some evaluation of their significance. Research personnel are therefore expected also to turn out material of a popular or semi-popular nature, as well as minor reports on techniques, methods, research outlines, translations, abstracts, informational leaflets, raw data reports, and so forth. Although none of these latter reports can take the place of the technical report, they are of undoubted value, and the authors deserve credit.

This leads us to the crux of the problem. Simply stated it is, "How do we determine whether progress is satisfactory?" Research progress cannot be measured in terms of dollars spent, laboratories built, or file cases stuffed with observations. Essentially a mental discipline, it cannot be sequestered or evaluated until transposed to paper. Only by evaluation of the written report, the final product, can we judge whether progress is satisfactory. Furthermore, in practically all cases in which research projects have for any reason been abandoned before a final report was written, a waste of funds has resulted. The published report then, of necessity, will be used as our yardstick of progress.

The problem now resolves into the determination of two things: (1) How much effort went into the production of a report, and (2) What is the relative worth of any individual report.

Money alone is a poor yardstick of effort. It often costs more to perform a stated amount of research in one locality or discipline than in another. Whether to continue the more expensive operation usually remains a policy decision. However, in judging performance at any two locations it would be patently unfair to judge effort by the amount of funds. This becomes especially noticeable when comparing costs of inshore research with mid-ocean research entailing large vessels and crews.

Facilities in terms of offices, laboratories, and vessels are not readily comparable. The nature of the problem largely determines the cost of the necessary facilities. A biochemist requires a well-equipped chemistry laboratory, a field biologist may occupy a small office, but require a car, a small vessel, perhaps field aids. In each case the researcher is provided with the means, whether cheap or expensive, to perform experiments or gather field data in order to solve a particular problem. In judging research production then, we must assume that each researcher has been provided with facilities in accordance with his needs. When production is below standard, facilities should be scrutinized, since research facilities are rarely fully adequate.

Since we have eliminated both funds and facilities, there remains the research man himself as our unit of effort. Because research is primarily a mental process, the bottleneck to production at many laboratories is the small number of scientists with the ability to analyze raw data, devise adequate tests of hypotheses, make logical deductions, and then convert these conclusions into intelligible reports.

Use of the scientist himself as the unit of research effort entails the question of whether or not we should recognize categories of effort, say between junior

and senior scientists. The use of categories is difficult for many reasons: different research groups have a different number of categories, and promotion and salary rates vary so that it would be difficult to establish comparable ratings. Moreover, ratings do not necessarily reflect either ability or experience. Although productivity usually increases with time, it often reaches a peak; thereafter it may tend to decline as the researcher—now an incipient administrator—is given more and more outside duties. Moreover, the length of time spent in each grade will vary with availability of funds. Examination of publication records indicates that it normally takes about 4 to 5 years for a man to reach a high rate of productivity.

Having decided on the scientist as the unit of research effort we come to the difficult task of deciding on the method of evaluating publications produced by the researchers. Because of the difficulty of evaluation, there has long been a tendency to rate scientists on the number of published articles. However, the mere enumeration of titles is almost worthless in assessing production. Some titles represent but a few hours of work; others are the culmination of several years of dedicated endeavor. To place them on the same footing is to make a mockery of science and discourage honest diligence.

Thus it is understandably discouraging to the dedicated research worker to read an announcement that so and so, who has just been hired, promoted, or given some honorary post, has published 50 or 60, or perhaps 80, scientific articles. After racking his brain the poor worker can remember perhaps three or four articles. Where did the rest come from? If we allow for some overpublicity, we may find the list was actually only 45 articles. Ten were semipopular articles in trade journals, another 10 were short notes on species distribution, perhaps 8 were general science notes in the journal of a local academy of science, 4 or 5 were published as abstracts (meaning an article on the subject may be forthcoming someday, if and when), several were processed (often merely a polite term for mimeographed) reports that never got far beyond the local office, the remaining 8 or 9 articles may have included 2 or 3 really worthwhile scientific contributions. This is not an attempt to indict the voluminous writer, but merely an example of how the use of false values in measuring research production may sometimes lead to erroneous conclusions.

In evolving an objective method for rating publications of research personnel, it should be emphasized that the primary function of research is to produce new knowledge. As a consequence, stress is placed on those articles which lay the foundations for new facts or principles. If a research worker can obtain sufficient publication credit by putting out progress reports and semipopular filler, he may never be persuaded of the necessity for concentrating on the kernel of his subject.

There will always be some criticism of any method of rating publications because their valuation is somewhat dependent on the point of view of the appraiser. Ratings must also bear some relation to the effort required to produce them. By effort, we do not mean physical labor; we reiterate that research is a mental process. After some study, I have evolved a system that attempts to encourage the writing of good technical reports, at the same time giving credit for all types of articles related to research.

The reports have been grouped into six categories based largely on content as follows:

Category A:

Original research requiring extensive analysis or original thought published in a scientific journal, or as a textbook or reference of college level. May include articles describing original techniques and apparatus.

Category B:

Research employing known techniques such as stream surveys, censuses, routine sampling when analysis is not extensive. Includes doctoral dissertations, revisions of textbooks or references, and taxonomic descriptions, keys, or reviews.

Category C:

Narrative and informational reports of scientific merit not requiring analysis. Includes general books or chapters on conservation, encyclopaedia articles, and technically correct information bulletins.

Category D:

Reports designed to make raw data available which may include short descriptions of methods and procedures but no analysis. Includes bibliographies, faunal lists, and glossaries.

Category E:

Semi-popular and popular articles, short descriptions of research programs, summaries of research accomplishments.

Category F:

Short faunal notes on species range, etc., critical book reviews, articles published only as abstracts, technical research notes in annual laboratory or commission reports, semipopular articles published in newsprint journals (not in newspapers).

The division of page credit between authors for multiple-author reports is shown in Table 1.

TABLE 1

PER CENT OF PAGES CREDITED TO EACH AUTHOR TO THE NEAREST ONE-HALF PAGE[1]

Number of authors	Position of author's name 1	2	3	4	5
1	100				
2	60	40			
3	50	30	20		
4	40	30	20	10	
5	40	30	20	10	0

[1] In case of a tie the extra one-half page belongs to the more senior author.

To obtain adequate material for a study of research production we have analyzed the publications of 60 scientists of the Fish and Wildlife Service during the 17-year period from 1940 to 1956, inclusive. No one was included with less than 10 years of work during the period; 32 worked for the entire 17 years.

First we determined the relative number and length of publications by type (Figure 1 and Table 2). This shows that out of 896 articles (solely or partially authored by one of our sample) 64 per cent were published outside of the Service. However, the articles published outside averaged but 12 pages in

TABLE 2

ACTUAL PAGE LENGTH OF ARTICLES BEARING NAMES OF THE 60 SCIENTISTS SAMPLED

Pages	Category A			B			C			D			E			F			Total		
	FW	O	T[1]	FW	O	T	FW	O	T	FW	O	T	FW	O	T	FW	O	T	FW	O	T
1-5	20	33	53	27	9	36	34	15	49	2	1	3	5	114	119	7	116	123	95	288	383
6-10	15	59	74	21	22	43	23	10	33					27	27		3	3	59	121	180
11-15	5	28	33	5	12	17	5	6	11	2	1	3		2	2				17	49	66
16-20	13	18	31	7	8	15	7	1	8	3	1	4		4	4				30	32	62
21-30	16	16	32	8	13	21	9	3	12	6	1	7		1	1				39	34	73
31-40	6	6	12	4	12	16	3		3	2	3	5					1	1	15	22	37
41-50	3	2	5	5	4	9	2	1	3	1		1							11	7	18
51-60	7	1	8	1	3	4				3		3							11	4	15
61-70	3		3	3	2	5	1		1	1		1							8	2	10
71-80		4	4	4	1	5				5		5							9	5	14
81-90	3		3	1		1													4	0	4
91-100				2		2				1	1	2							3	1	4
101-110	1		1	4		4	1	1	2	7		7							13	1	14
> 110	3	2	5	1	3	4	1	1	2	5		5							10	6	16
Number	95	169	264	93	89	182	86	38	124	38	8	46	5	148	153	7	120	127	324	572	896
Per cent	36	64		51	49		69	31		83	17		3	97		6	94		36	64	
Ave. No. Pages	27	15		25	24		14	16		63	32		3	5		3	3		26	12	17

[1]FW — Fish and Wildlife; O — Other; T — Total

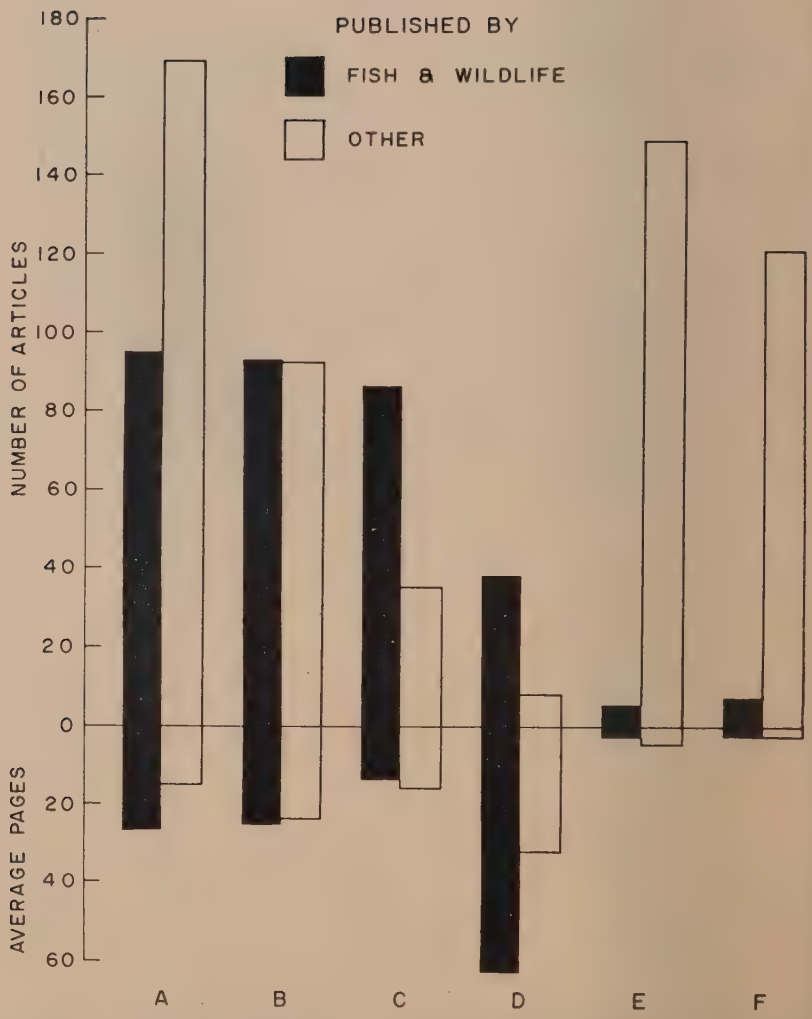

FIGURE 1. Number and length of articles by categories bearing the name of one of the selected group of 60, 1940-56.

length compared to 26 pages for Service publications, so that the Service actually published 56 per cent of the pages. Of the articles requiring most research analysis (A Category) the Service published only 36 per cent of the articles, but 50 per cent of the pages.

The great number of very short articles in the E and F categories (which do not require extensive research) demonstrates that number of articles published would be a very unreliable index of research production.

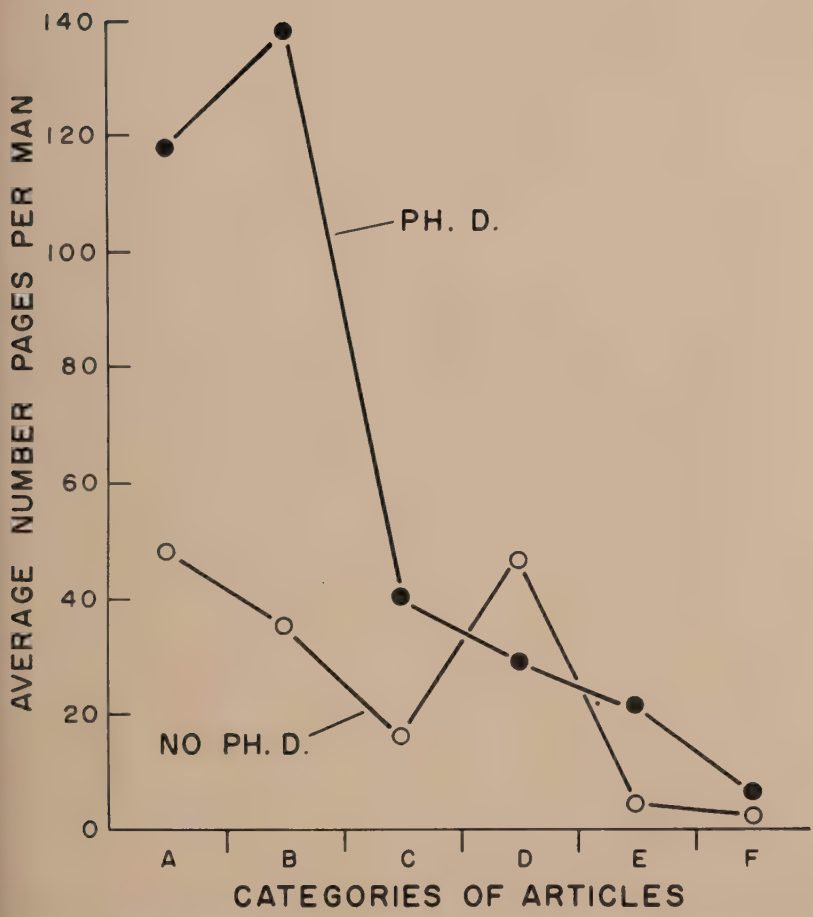

FIGURE 2. The average number of pages according to category, published per man on a 17-year basis by scientists with and without the doctorate.

That the number of pages published is also not too reliable an index is shown by the great length of the articles in Category D, which are chiefly raw data. It should be observed that only 16 of our sample of 60 published an article in this category. This is the only category in which those with Ph.D.'s published less pages per man than those without (Figure 2).

Obviously neither number of articles, nor number of pages can serve as an index. The number of pages published would be fairly reliable if it were not for the great variation between categories in the value of the product. The only practical solution is to use the number of pages weighted by categories according to their relative contribution to research.

TABLE 3

ADJUSTED PAGE CREDITS OF 60 SCIENTISTS BY ACADEMIC TRAINING AND FIELD OF WORK

Adjusted page credits	Without doctorate degree				With doctorate degree				Total	
	Anadromous	Inland	Marine	Other	Anadromous	Inland	Marine	Other	Without doctorate	With doctorate
0-200	6	1	1	1					9	
201-400	4	1	2						7	
401-600	5				1				5	1
601-800	1	2	2	1			1	1	6	2
801-1000			2	1		1	1		3	2
1001-1500		1	2			3	2		3	5
1501-2000			2			1	1	1	2	3
2001-2500		1	1		1	1			2	2
2501-3000			1	1			1		2	1
3001-4000						1	1			2
4001-5000						1	1			2
5001-6000										
6001-7000								1		1
	16	6	13	4	2	8	8	3	39	21

The relative weights of each category employed in my analysis are:

A - 10
B - 5
C - 3
D - 0.5
E & F - 2

The compilation and listing of raw data, the tedious and meticulous listing of bibliographic references, or the listing of species distributions require care and exactitude but not deep scientific thought. It must also be remembered that practically every good research paper sprang from a large quantity of raw data that had to be meticulously listed and tabulated prior to the actual analysis for the research paper. Because some of these original data are made available (almost universally now by photo reproduction) in multilith form, hardly entitles the author of a 25-page research paper to claim much credit for releasing 250 pages of listed data. On a basis of 10 credits per page for Category A material the per-page credit for Category D has been set at 0.5.

Categories E and F differ somewhat in content but agree in their brevity; 86 per cent of 280 articles were under 6 pages and only 3 per cent were over 10 pages. These have been given 2 credits per page.

The ratings of the 60 scientists according to academic training and field of work (Table 3 and Figure 3) show clearly that those with the doctorate averaged considerably higher than those without. Thus 69 per cent of those without, rated less than 800 credits compared to only 14 per cent of those with the doctorate.

It is noteworthy that the anadromous non-doctorates rated very low. This is perhaps partially explained by their over preoccupation with the gathering of field data because of the pressure of management problems in Alaska and on the Columbia River. Data alone cannot answer questions. It must first be subjected to careful analysis.

Perhaps the chief difference between the production of the different groups lies in the approach. The first work on a new problem is usually exploratory in nature. Some investigators can never carry their problem past this stage because they are unable to form hypotheses concerning the problem. Or, if they form hypotheses, they attempt to prove their validity or invalidity with haphazardly collected data rather than through systematic observations pre-designed for use in testing their hypotheses.

This difference of over two orders of magnitude in individual production is truly astonishing. How did it come about? What causes it to continue? And, what is the remedy?

The production of research results depends on at least five factors:

1. Ability. Research requires a special kind of ability. Many intelligent people are miscast in a research role because either they lack intellectual curiosity, or they are unable to do the concentrated disciplined thinking required.

2. Training. Research requires good training. We cannot afford to start every problem with crude experiments and repeat every mistake of the past. Research requires a special type of training. Too many colleges are teaching men how to collect material and analyze it by already standardized techniques

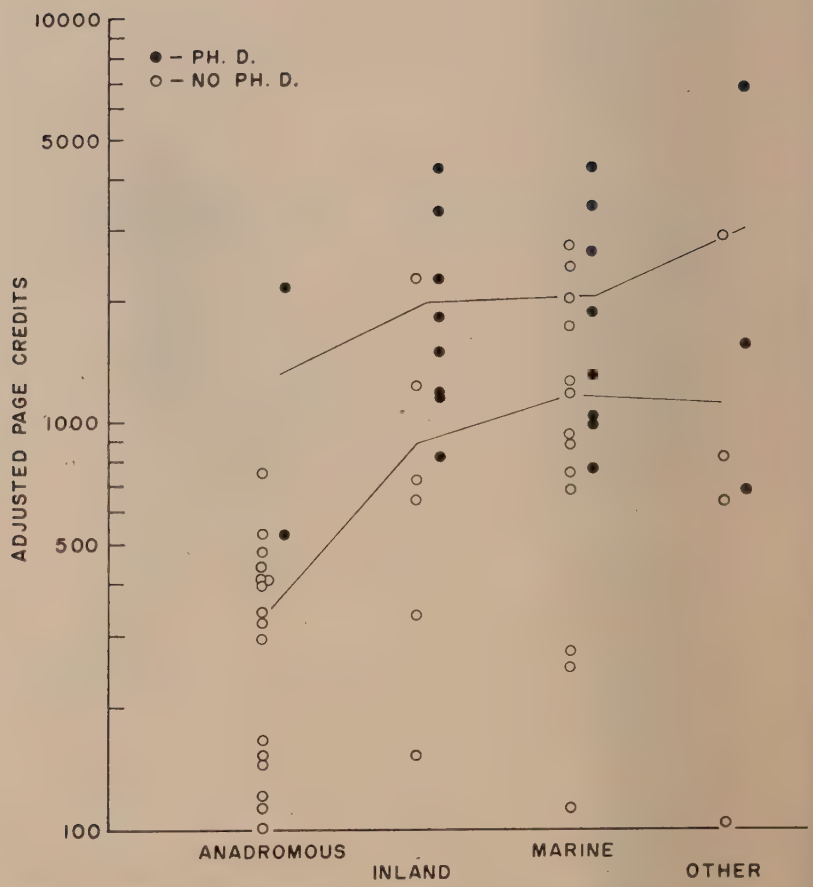

FIGURE 3. Page credits adjusted by categories, shown according to training and field of work, for the 17-year period.

without teaching how one goes about the intellectual probing necessary to solve a new problem. The result is the turning out of numbers of skilled workmen or technicians if you please. They are helpful up to a point, but many never achieve the ability to solve problems.

3. RESEARCH CLIMATE. This factor, often ignored, is of the greatest importance. Junior men of ability may wither or develop according to their scientific associations and the type of leadership furnished them. Junior men forced to work at lonely field stations often lose their interest at a time when stimulation is most needed.

4. PHYSICAL FACILITIES. Research is costly and requires the best of facilities. Carrying out a program of research without adequate physical facilities is not

economical. If facilities are inadequate for solution of a problem, it is wiser not to attempt it rather than to siphon off money always needed elsewhere. Striking examples of this lack are laboratories that are in reality only offices, with no provision for study of living material; research vessels that are cast-off hulls partially adapted for hydrographic research at great expense, yet not suitable for the job; and field stations so poorly devised for living that men spend precious time in merely managing to exist.

5. Adequate staffing. It is essential that there be some relation between the size and training of the available staff and the problems they are expected to solve. If the staff is too small or lacks certain specialization, an effort should be made to reduce the immediate goals to those than can be met. An attempt to study at one time all ramifications of a large problem may be very frustrating. If a problem cannot be broken into small enough self-contained phases that can be tackled one at a time with reasonable assurance of progress, then the problem should be shelved until adequate staff is available.

We have noted the great range in apparent productivity of individual investigators and have discussed some of the factors involved. The obvious question posed is: Can some of these factors be changed so that production is increased? We believe they can.

Concerning the first factor, ability, we submit that since research is largely a mental process, it requires much higher than average intelligence. Out of the many workers hired, only a few are of research calibre. Yet because of the compartmentalization of an organization, a man hired to do research is continued in research even though it finally becomes apparent that his services could be more advantageously employed in other phases of conservation work. Part of the difficulty arises from the fact that an insufficient proportion of those of higher intelligence are attracted into research. Part of the problem arises from the fact that it is extremely difficult to judge during his first year as an investigator whether a man will turn into a research worker. After the first year, at which time he obtains permanent status in our Service, the tendency is to continue advancing a man without due regard for his productive capacity. Indeed, since it is normal for junior scientists to collect and compile data and work under rather immediate supervision, it may take some time before it is realized that he lacks originality or perhaps the ability to transpose ideas into actual reports. A weeding-out process for selection of those who should continue in research should be made at intermediate levels. Those not adapted to research should then be transferred to other activities. Most of these people are sincere, hard-working employees who can contribute in many fields but lack that certain quality demanded by research.

Training is certainly an important factor in research. As shown in Figures 2 and 3, men with the doctorate averaged about twice as much in publication credit as those without. It will be noted, however, that in the marine field many without doctorates were close to the top. Many of these have had up to as much as two years of graduate training without taking a doctorate. There are thus indications that although good research men will perform well despite lack of graduate training, extra academic training confers a distinct advantage. Part of the reason for the higher average of those with doctorates may lie in the selection process of the universities themselves. Most universities of high standing accept only the better students as doctoral candidates, and many never

succeed in attaining their degree. The Fish and Wildlife Service has recognized this need for advanced training in the program just adopted for permitting selected employees to attend universities for graduate work at Service expense.

RESEARCH CLIMATE is not easily defined but is a rather essential ingredient. A man of intellectual curiosity, given a challenging problem, adequate equipment and library facilities, and association with other research workers, will usually produce to the limit of his ability and training. The kindling and maintenance of genuine interest are greatly augmented by his associations. This is why a large group of researchers, containing specialists in several related disciplines, normally can boast of a higher production per man.

PHYSICAL FACILITIES are costly to acquire and maintain, yet without certain facilities some problems can never be solved. Because of the cost, it is not possible to equip an unlimited number of laboratories with seagoing vessels, adequate libraries, chemical and bacteriological laboratories, large sea-water systems, and reference collections. There is often pressure by well-meaning people to build new laboratories in new locations. In only a few specialized cases are these justified. The Fish and Wildlife Service now has a number of strategically located laboratories, and these should be fully equipped before any more are seriously considered. Furthermore, the overhead cost is proportionately much less on larger installations.

ADEQUATE STAFFING means that each problem studied should be assigned the number and type of personnel required. This presents many difficulties since some problems require specialists in very circumscribed fields. Where a problem promises to be of long duration, or at larger laboratories where problems of the same type are likely to recur, the hiring of specialists in narrow fields is often justified. For short-term problems the Fish and Wildlife Service has more recently met this problem through contract research with institutions having specialists in the required fields.

In summary, the analysis of publication records of 60 Fish and Wildlife Service scientists over a 17-year period shows a tremendous range in research production. A portion of this difference can be ascribed to the higher production rate of those with advanced academic training, and the lowered production of those closely associated with specific management responsibilities.

Suggested measures to raise production include the transfer of intermediate grade research employees who are low in research production into other fields of activity within the Service. The new Fish and Wildlife Service policy of providing opportunity for advanced academic training of selected employees is heartily endorsed. The provision and maintenance of adequate facilities by concentrating personnel in existing laboratories is recommended.

OBSERVATIONS OF MOLTING FEMALE KING CRABS, *PARALITHODES CAMTSCHATICA* (TILESIUS)

by

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ABSTRACT

This report describes observations of nine molting mature female king crabs, *Paralithodes camtschatica* (Tilesius), caught in Pavlof Bay on the Alaska Peninsula between May 1 and May 18, 1957. Observations show that molting soft-shelled crabs emerge through an opening between the posterior margin of the carapace and anterior margin of the abdominal segments. The female king crab specimens all cast their shells without males being present. Most cast shells were intact, without breaks in the shell parts. Maximum increment in carapace length of newly molted female king crabs was attained two days after molting and ranged from 2 to 6 mm.

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INTRODUCTION

The King Crab Investigation of the United States Bureau of Commercial Fisheries is conducting studies to determine the need for conservation measures of eastern Bering Sea king crab, *Paralithodes camtschatica* (Tilesius), as part of the research program of the International North Pacific Fisheries Commission. In this respect, knowledge of the biology of king crab is essential.

Molting, an important phase in the life history of king crab as well as in other crustaceans, is a phenomenon whereby the exoskeleton is periodically discarded. Generally, all outer cuticular layers of the shell, eyes, antennae, gills, tendons, mouth parts, esophagus, and stomach with its chitinous teeth are replaced. In mature female king crabs, molting is associated with reproduction and growth. It is generally accepted by researchers that molting occurs annually, followed immediately by mating. The fertilized eggs are carried for approximately 10 to 11 months, after which hatching takes place and molting and mating are again repeated. Marukawa (1933) reports that female molting is aided by the male crabs who hold the chelipeds of females during molting and mating. He also reports that molting can take place in the absence of males.

This report describes observations of nine molting female king crabs caught in Pavlof Bay on the Alaska Peninsula between May 1 and 18, 1957. Work was done aboard the M. V. *Deep Sea*, a king crab factory ship.

I am grateful to Wakefield's Deep Sea Trawlers, Inc., and the crew of the vessel for their cooperation and use of their facilities. My thanks also to Mr. Glen Davenport for his assistance, and Mr. T. O. Duncan for photographs.

PREMOLTING OBSERVATIONS

Nine female king crabs captured with an otter trawl were placed in live boxes provided with running sea water. For identification each crab was marked with a number on the carapace before and after molting. Carapace length measurements, taken from the hind margin of the orbital socket to the median indentation of the posterior margin of the carapace, were made daily from time of capture until release.

All specimens exhibited premolting characteristics. Shells of the carapace and appendages were thin and pliable. The membranes connecting the shell parts were also very thin and cellophane-like in texture. A slight pink color, differing from the white found in crabs of nonmolting condition, was detected under the thin membranes at joints of each leg and between plates of the abdomen. On one specimen the suture along the anterior margin of the first abdominal seg-

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Bulletin 5, Int. North Pac. Fish. Comm., August, 1961.

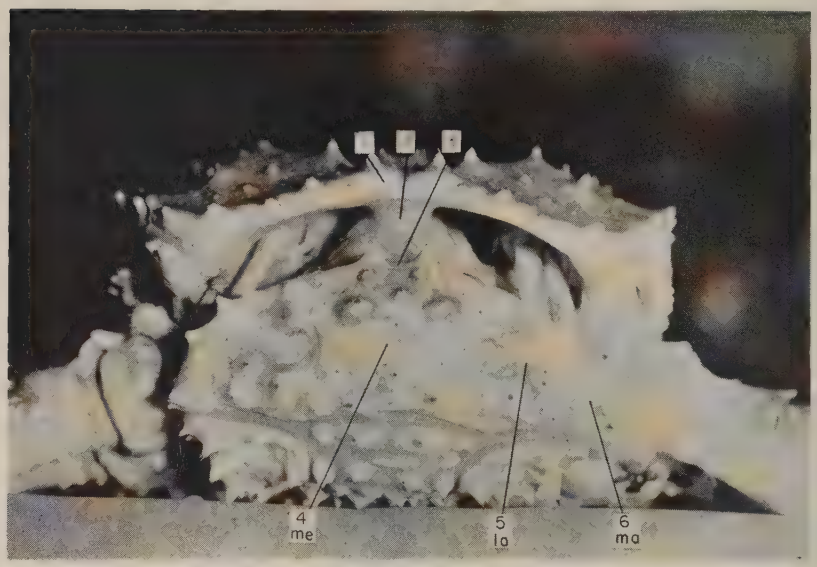

FIGURE 1. Posterior view of king crab showing arrangement of carapace and abdominal segments (After Marukawa, 1933).
1—posterior margin of carapace ;
2—isthmus between carapace and body ;
3—first abdominal segment ;
4–6—second abdominal segments.
me—median plate ; la—lateral plate ; ma—marginal plate.

ment was split and the pink soft shell exposed. (See Figure 1 for arrangement of abdominal segments.) The eyes of specimens were bright red in contrast to brown colored eyes of nonmolting crabs.

Prior to molting, female crabs were observed with their bodies lifted off the bottom of the live boxes. Their abdomens, extended away from their bodies, moved rhythmically back and forth exposing swimmerets covered with empty egg cases. This behavior was seen frequently until molting and may be beneficial in releasing zoea larvae as well as loosening the soft new shell from the old, making extraction easier during molting.

MOLTING OBSERVATIONS

The first step observed in molting was a separation in the thin membrane anterior to the first abdominal segment. The carapace and abdominal segments then started to part, thus tearing the membrane further and opening a large gap. The tear in the membrane extended completely along the anterior margin of the abdominal segments, vertically up the isthmus between the carapace and body, and completely across the posterior margin of the carapace. As the membrane continued to tear, the opening grew larger and the soft-shelled crab backed out of the old shell. During the only occasion when a crab was timed casting its shell, four minutes were required to back out of the old shell.

Many females examined during trawling operations were found with the membrane along the first abdominal segment split and this section open.

POSTMOLTING OBSERVATIONS

Seven of nine cast shells remained intact (Figure 2). In the other two, thin membranes in other calcareous parts were torn.

Outer layers of antennae, eyes, gills, stomachs, tendons of legs, and mouth parts were left entirely with the old shells. One specimen sloughed off its left fourth leg at its basal segment and left it in the cast shell. This crab would probably regenerate a new leg.

Three to four days were required for the carapace of newly molted crabs to harden. Although specimens were held from 5 to 13 days after hardening, the initial growth measured two days after molting was found to be the total growth. Carapace length increments ranged from 2 to 6 mm., with an average of 4 mm., as shown in Table 1 and Figure 3.

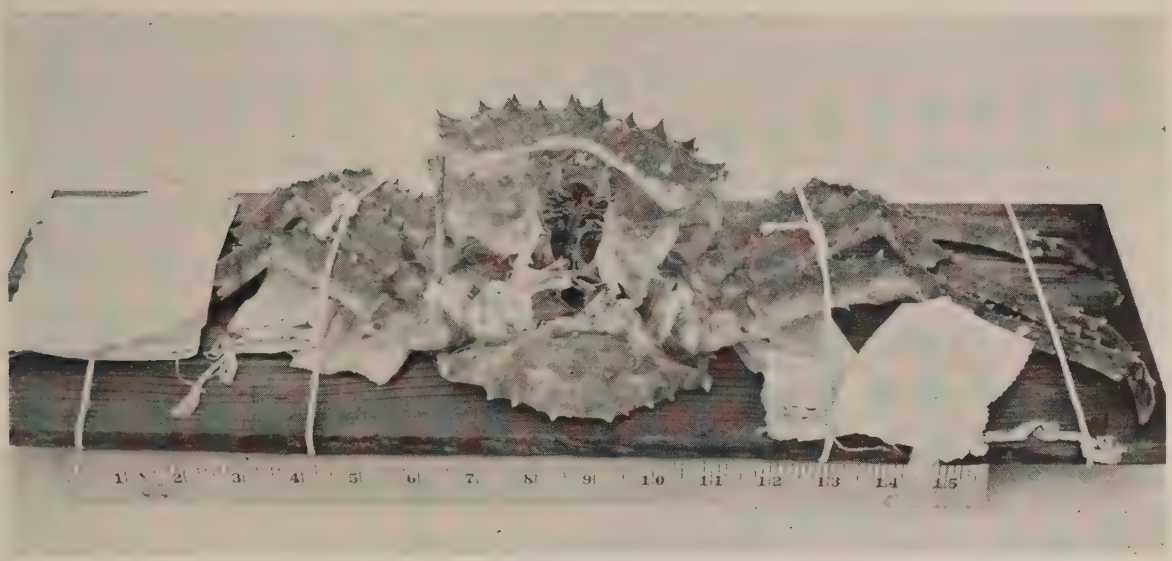

FIGURE 2. Posterior view of intact cast shell of female king crab showing opening through which the crab emerged from the old shell.

TABLE 1. Dimensions of nine molting female king crabs.

No.	Carapace length before molt (mm.)	Carapace length after molt (mm.)	Growth increment (mm.)	Carapace length increase (%)	Days held from molt to release
1	115	120.0	5.0	4.3	10
2	118	121.0	3.0	2.5	13
3	119	122.0	3.0	2.5	10
4	120	122.0	2.0	1.7	13
5	123	127.0	4.0	3.3	11
6	127	132.0	5.0	3.9	7
7	131	136.0	5.0	3.8	13
8	131	137.0	6.0	4.6	5
9	141	144.5	3.5	2.5	12

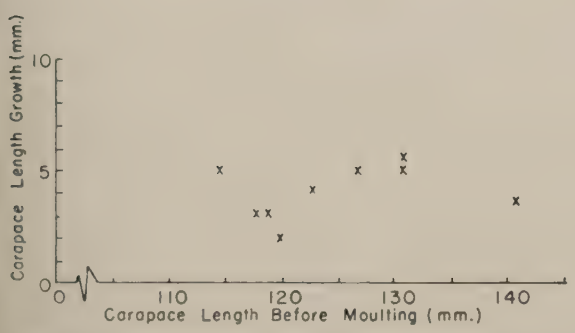

FIGURE 3. Growth increments of nine female king crabs.

Except for one specimen, all newly molted females failed to extrude eggs.

DISCUSSION

The observations of molting mature female king crabs made in this study were similar to that described by Marukawa (1933).

Wallace *et al.* (1949) states, "A simultaneous action is exerted by the tissue under the carapace, leading to breaks on the sides, posterior end, and, in some cases, entirely across the carapace. Very often the old shell is left completely intact except for the breaks along the sides of the carapace." In the present study seven cast shells remained completely intact, except for torn membranes on the posterior ends of the carapaces. In all nine cast shells the carapace and leg shells were not cracked.

Growth increments from this study agree with growth of females described by Marukawa (1933), Wallace *et al.* (1949) and Stevens (1955). The 3 to 4 days taken for shell-hardening also agrees with Marukawa's findings.

Wallace *et al.* (1949) states that female king crabs allowed to molt in the absence of males do not extrude their eggs until permitted to mate. In this study, however, one of the nine females extruded eggs a day after molting. It is known in other crustaceans that females may extrude unfertilized eggs which later disintegrate.

SUMMARY

1. Before molting female king crabs were observed

rhythmically moving and stretching their abdomens.

2. The female crabs molted without males being present.

3. Most of the shells cast were intact except for the split in the membrane connecting the carapace to the abdominal segments.

4. One molting process was timed at four minutes.

5. All but one of the newly molted females failed to lay eggs.

6. Size measurements varied during shell-hardening; however, the growth measured two days after molting was the total growth.

7. Amount of growth ranged from 2 to 6 mm., with an average of 4 mm.

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J. F. T. Saur (U. S. Bureau of Commercial Fisheries, Biological Laboratory, Stanford, Calif.), *On the Differences between Sea Water Temperatures from Ship's Weather Observations and Sea Surface Temperatures.* Injection temperatures constitute a major source of historical oceanographic data for the open ocean. To assess the reliability of these data, special 'bucket-sampled' sea surface temperatures were obtained by U. S. Weather Bureau Observers aboard five MSTS ships in the Pacific for comparison with the normally reported injection temperatures. Statistical analyses of each of the 33 sets of data were made to determine (*a*) the average difference between the surface temperatures and the injection temperatures and (*b*) the distribution and standard deviation of the differences of paired observations. The analyses indicate that each ship has its own average bias of injection temperature, probably due to the construction and operation of the water injection system and to the errors in the commercial-grade thermometers used in the system to measure temperature. The averge bias for each ship was as follows: 1.4°, 1.3°, −0.5°, 1.7°, and 2.0°F. The standard deviation of the differences of paired observations was relatively consistent between ships, being about 1.2°F. Indirect evidence suggests that for some ships a portion of this variability may be that the routine measurement of injection temperature in the engine room is not made at the same time and position as the weather observation with which it is reported.

PROBLEMS IN FISH POPULATION FLUCTUATIONS

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Our chairman has defined "fisheries oceanography" meaning "any kind of oceanography required for e appraisal or exploitation of any kind of organism eful to Man". This, as intended, is a very broad finition. My contribution to this symposium will be nfined to a discussion of only one particular set of oblems that I believe to be most important in the ilization of fishery resources and afford most ex- ing opportunities for oceanographic research— mely, fishery fluctuations.

By fishery I mean any harvesting of any living ean resource, and by fluctuations I mean any irregu- rity in the amount or the quality of the harvest. nce most of our present commercial harvest from the a consists of fish, my discussion, terminology and ex- nples pertain to fishes, but most of the concepts are so appropriate to the invertebrates and some even to e flora of the sea.

In considering the problem of fishery fluctuations I ve come to realize that there are a great many rallelisms in the discipline and the state of knowl- ge in fishery biology with those in oceanography. fishery biology I mean the study of fish populations dynamic systems—and by oceanography I mean the rallel thing: The study of the ocean as a dynamic stem. In defining each of these in this way I am noring a great deal that could be included, but I lieve I am retaining the central core of each.

The first parallelism is that there are only a few ings we can measure. In fishery biology we measure ly the fisherman's harvest and the effort he puts to making it, when we really want to know the size the fish population and how fast it is changing. In eanography we can only measure the temperature d salinity when we want to know which way the ater is running, and how fast. To be sure, in each ld we can, by a one-time special effort, get a direct easure (estimate). We can lay a tag-and-recapture oject—or a multiple-ship drogue expedition. But ese are not routine, every-day events. For the most rt we have to deduce what we want to know from mething else that we can measure.

Second—and this is largely a consequence of the st—for fish populations we have only a theory to l us how a fish population reacts to fishing. This lates to a fish population living in a steady environ- nt. In some few instances, and for a limited period time, we find that a population really does react proximately as the theory says it should. For ocean- raphy we have more theories. But practically all re- e to an equilibrium ocean. For some parts of the ean, sometimes, one of these theories, or a combina- n of them, seems to explain approximately what tually happens.

Of course the trouble with the theory of fishing is that a fish population reacts to other things besides fishing—things in the variable environment. We assume these things average out—and sometimes they do. But often the time dimension for averaging out is intolerably long. And of course the same thing is true of the ocean. Over a long enough period of time the average ocean probably is an equilibrium ocean, but the measurements we take must be mostly those of an ocean in disequilibrium. I believe it can be said for fishery biology, as it has been said for oceanography, that there is a peculiar dreamlike quality characterizing our descriptions and discussions of the things that we are studying.

As a fishery biologist I venture the further thought that it would be easy to relax and enjoy this dream were it not for fluctuations. They have a nightmare-ish quality that jolts one into reality. And I am reminded that this could be true for oceanographers as well. A year ago this month a group of oceanographers (including the one who first voiced the phrase "peculiar dreamlike quality"), meteorologists, marine biologists, and fishery biologists met at Rancho Santa Fe, bringing with them meteorological, oceanographic, biological and fishery data, to describe what happened in the Northeast Pacific Ocean in 1957 and 1958 and why. It was abundantly clear that there had been a sudden and marked warming of at least the eastern margin of the Pacific from Alaska to Peru, with an assortment of consequences to the oceanic biota. The results of pondering over these events will be published and I will not here attempt to put them before you, except to remark that we still do not know, with any precision, what happened, nor with any degree of assurance, why.

Henry Stommel, in his book on the Gulf Stream, has this to say about fluctuations: (Stommel 1958, p. 136)

> "Many catastrophes of an economic kind, such as the failure of the rice crop in Japan, or of a certain fishery, or years of unusual numbers of icebergs in shipping lanes, are attributed to fluctuations in ocean currents. Very little is really known about such fluctuations. It takes years of careful and expensive observation to produce even a very crude description of them. The scientific programs of our oceanographic institutions are not geared to long-term problems of this kind; there is much pressure for novelty, much temptation to follow the latest fad, and a persistent though erroneous notion that all worth-while problems will eventually be solved by some simple, ingenious idea or clever gadget. A well-planned long-term survey designed to reveal

fluctuations in ocean currents would be expensive and time-consuming. It might even fail, because of inadequacies of the tools we have at hand. But until this burdensome and not immediately rewarding task is undertaken, our information about the fluctuations of ocean currents will always be fragmentary."

Henry Stommel seems somewhat overwhelmed by the task of making the observations needed for describing and elucidating fluctuations in the Gulf Stream. The task probably is even more difficult for describing and elucidating the fluctuations in fish populations, because it is likely that the effects on fish populations of physical and chemical changes in the environment are mediated through several trophic levels in the biota. We will come back to this later.

It seems clear that the problem of fluctuations lies at the research frontier in both fishery biology and oceanography, and that it is going to be difficult to break through the frontier.

Let us consider again, for a moment, the anatomy of fishery fluctuations. We can discern three principal elements operating to determine the amount of the catch: The abundance of the organism, its availability to the harvester, and the amount of harvesting effort. We shall not here be concerned with the last of these. The amount of harvesting effort is determined by economic conditions. Changes in the amount of effort can be measured, though not easily, and its effects on the amount of catch can be determined and discounted. It is not a problem in biology or oceanography.

Abundance and availability, in contrast, present problems both in biology and oceanography.

We suspect that availability varies widely. For instance, the failure of the albacore fishery from 1928 to 1938 was, we think, an availability phenomenon. The albacore population probably was as large as usual, but did not approach close enough to the coast to enter the range of the fishing fleet.

Availability is a matter of distribution and behavior, both on a coarse-grained pattern as in the albacore failure, and on a fine-grained pattern as in the schooling of fish. It is highly important to the strategy of fishing and to the economy of the fishing industry. Since Professor Uda will, I think, discuss availability in some detail later in this symposium, I shall confine myself to fluctuations in abundance (population size).

Fishing theory says that the annual increase in a population is a function of population size and environmental capacity. If a population "fills" its environment, births and deaths are equal and the population is in equilibrium. When fishing takes place, catch mortality is imposed, the population is reduced below the environment's capacity, births exceed "natural" deaths and the population tends to increase toward the environmental limits. With very intense fishing and a very low population level, the reproductive increase is near its maximum, natural mortality near its minimum, but the annual increase is low because there are few spawners. When fishing is very light and the population near the environmental limits, the spawning population is large but the bac pressure from the environmental limit depresses production or increases natural mortality, or both, that the annual increase is again small. At some lev of population size intermediate between these tremes, where the spawning stock is moderately lar and back-pressure from the environment moderate gentle, the annual increase is maximal. Of course, any level, the population size will be in equilibriu when the annual catch equals the annual increase, b the annual harvest that can be sustained without d turbing the equilibrium will be maximal at the le of population abundance that affords the maximu annual increase.

Fishery biological research has been directed mair toward determining this level of maximum sustainal yield, using the concepts embodied in this theory. number of mathematical models have been develop to express these concepts. They assume that the vironmental capacity is constant or fluctuates mod ately and randomly, and that the observed or co puted changes in recruitment and mortality and hei annual yield are functions of population size density) alone. These models have proved very use in studying the population dynamics for some fisheri

In other populations, including some that supp very important fisheries, the effective birthrate, t is, the relative numbers reaching recruitment a varies widely from year to year, apparently withc relation to the size of the spawning stock. This known by studying the age composition of samp of the catch. From the data on age composit through sufficient number of years, it is possible estimate the relative number of individuals survivi to fishing size or age from each year's spawning shall call this relative number "year-class strength

I have looked up a few data on relative year-cl strength:

	Successive year classes	*The largest was*
Western Atlantic mackerel	among 14	15,000 times the smal
Eastern North Pacific sardine	21	700
Kodiak (Alaska) herring	28	34
Southeast Alaska herring	20	13

These are all very gross estimates, and should taken only to indicate that year-class strength of varies through several orders of magnitude.

Year-class strength obviously must be a function number of eggs spawned, or of survival through egg stage, through the planktonic larval stages through the post-planktonic juvenile stages, o combination of these. No doubt irregularities oc in all stages, but the evidence, still regrettably sca points to the survival through planktonic egg larval stages as being the most likely critical on determining year-class strength.

Where year-class strength fluctuates widely i not a function of population size and we must to environmental causes.

How shall we do this?

Because it is difficult to speak in generalities, I ll employ an hypothetical example. Let us con- er a fish population of a species, like the mackerel, sardine or the anchovy, that spawns in the waters California.

Through evolutionary time, in the members of such sh population, there must have evolved an internal chemical system and a related pattern of behavior t determines the responses to the things sensed in environment. The behavior pattern must have n so adjusted that it lead to successful reproduc- n through all of the time involved in its evolution. herwise the species would be extinct. If I may speak ological, the members of a living fish population, at least the vast majority of them, must work out blems of navigation and prediction to enable them find and occupy a specific kind of water mass for wning.

This water mass must have physical and chemical perties which are tolerable to the biochemistry and physics of the eggs to be spawned and the larvae be hatched from the eggs. Further, by the time vae have hatched out, and by the time they have ly absorbed the yolk sac, this water mass must con- n other organisms suitable for the larvae to feed n and in such concentrations as will permit the vae to get enough food for maintenance of metabo- activity and growth. Doubtless the larvae will uire larger food particles or more of them as they w larger. So this water mass must continue to ord an increased and probably different diet ough the subsequent months of planktonic larval stence. Finally, when the larvae metamorphose into juvenile stage and take up an active, rather than assive, drifting existence, this water mass must e reached a place or a condition which is suitable juvenile existence. Many marine species spawn the open sea at a considerable distance from the enile nursery grounds. For such a species, the ent must have predicted the trajectory of the ter mass over a period of weeks or months.

To be sure, many individuals of the population may l to navigate properly or to predict accurately and seems that often the whole population, or most of may be in error. Or, alternatively, the conditions the sea may in some seasons become so anomalous t there are no water masses suitable for the species wning or the survival of the eggs and larvae after wning. In any event, there are many year-class lures or near-failures in our widely-fluctuating fish- s. Such failures, of course, must be interspersed h enough successes for the population to be per- nated. For species with an adult life of several rs, several annual failures can happen in succes- n, and apparently do happen in our widely fluctu- ng fish populations, without exterminating the cies.

have spoken of the water mass as a thing which intains its integrity over considerable periods of e. This probably does not happen often for water sses in the surface layer. They undoubtedly un- go changes through insolation and through mixing izontally and vertically with adjacent waters. In a sense, we could think of a water mass as undergoing an evolution as to its physical and chemical properties and also as to the trophic succession in its biota. Perhaps more frequently than not, the water mass may undergo dissolution instead of evolution and such cases may indeed lead to failure of survival of its larval fish population.

In this connection, it is interesting that there have been reported two instances in which it appears that a water mass was changed so rapidly that the contained fish larvae died almost immediately. One instance, reported by John Colton (1959), was of larvae contained in a mass or parcel of water at the southern edge of Georges Bank in which the temperature, apparently by mixing with Gulf Stream water, had risen rapidly enough to kill the fish larvae it contained. The other instance, reported by Donald Strasburg (1959), was the occurrence of dead larval Frigate mackerel in plankton tows in Hawaiian waters under circumstances suggesting water mixing as the cause. We do not know whether or not such sudden changes can occur in really large enough water masses to determine the failure of a year class, but these reports are suggestive.

However this may be, it appears that one mode of attack on the problem of year-class strength would be the study of the source, the life history, the movements and, perhaps the dissolution of water masses. This infers sea work to observe, with continuity through space and time, many properties of the water and its biota. It suggests, further, that a joining of the physical and biological disciplines might facilitate such a study. The joining of the laboratory experimentalists would probably facilitate the study still more. If we know what properties of the environment the fish is able to sense, and how the fish reacts to the things it senses, we would be led more quickly to observing the things which cause the fish population to maintain or change its distribution, and if we could identify in the laboratory the survival requirement of fish larvae, we would be led more quickly to our observing the critical events in the sea.

In effect, I am proposing the joining of four disciplines: oceanography, fishery biology, marine biology and experimental biology. Possibly additional disciplines may be required. Certainly, instrument systems for recording automatically, with time and space continuity, a number of properties of sea water and its motions would be of tremendous importance. On the biological side, it is quite possible that fish pathology, especially the study of fish larva diseases, may be germane to this study.

To speak in more general terms, it is my belief that in fishery oceanography the challenge and the opportunity lies in studying the changing sea rather than the equilibrium ocean, and in studying the biological consequences of the changes at the various trophic levels. In speaking of "consequences" I mean to include not only the effects on the population numbers, which I have dwelt upon at some length, but also on population distribution and behavior which Professor Uda will soon discuss with us. In the aggregate this implies the necessity of observation of phy-

sical and chemical properties of sea water, its motions and mixings, and the numbers, kinds and perhaps stages of the biota inhabiting the waters, all with space and time continuity sufficient to describe the events that take place and to investigate their interrelationships. The biological determinations probably would more readily be made with the aid of laboratory experimental determinations of environmental requirements critical for survival of the various organisms, particularly pelagic fish larvae.

It would seem that this amounts to an undertaking of such vast scale that it may be quite out of line with the importance of fishery resources to our society. However, fluctuations of the ocean and of its plant and animal populations is a problem of significance not only to fisheries. Modern military systems no longer can be based on the average state of the sea, and modern meteorology is no longer uninterested in the possibility that the feed-back to the atmosphere from anomalous sea conditions may have to be considered in extended weather forecasts. We can hope, therefore, that progress in the field does not depe alone on research activities in the interests of dev oping and utilizing fishery resources, but will ben also from activities undertaken in the interest other important activities of mankind.

An indication of trends in this direction is recent report of the National Academy of Scien Committee on Oceanography, which, among ot things, proposes a great augmentation of effort, mu of it along the lines we have considered in this d cussion.

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THE EFFECTS OF SALT SOLUTIONS OF DIFFERENT STRENGTHS ON OYSTER ENEMIES

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ABSTRACT

Boring sponges (Cliona celata), starfish (Asterias forbesi), and tunicates (Molgula manhattensis) were treated in salt solutions of different strengths for 1, 3, 5, 10 and 15 minutes. Oyster drills (Urosalpinx cinerea) were exposed to a saturated solution for 30 minutes, one hour and three hours. Sponges were killed by a 5-minute exposure in a saturated solution and by a 10-minute exposure in solutions 90, 70 and 60 per cent saturated. If sponges were dried following exposures, greater mortalities occurred. A one-minute exposure, followed by a one-hour drying period, was sufficient to cause complete mortality in solutions 100 and 90 per cent saturated, three minutes in 80 per cent saturated, ten minutes in 70 and 60 per cent saturated, and fifteen minutes in 50 per cent saturated. Starfish were killed by a 3-minute exposure in solutions 50 per cent or more saturated. Tunicates were killed by a 5-minute exposure in saturated and 90 per cent saturated solutions, 10 minutes in solutions 80, 70 and 60 per cent saturated, and 15 minutes in solutions 50 and 40 per cent saturated. Although drills, Urosalpinx and Eupleura, are not killed readily by salt solutions, embryos of both can be killed by treating them in a saturated salt solution. Caution should be exercised in exposing seed oysters (Crassostrea virginica) with damaged bills to salt solutions, since they are killed by high salt concentrations.

INTRODUCTION

Of more than a thousand chemical compounds tested at Milford Laboratory for their effects on shellfish enemies, none killed the boring sponge, Cliona celata, at concentrations low enough to be non-injurious to oysters. In the past, certain workers, including Dollfus (1921), deLaubenfels (1947) and Warburton (1958), recommended that sponges be killed by placing infested oysters in fresh or brackish water. Loosanoff (1945) reported that starfish can also be killed in sea water of reduced salinity. With both sponges and starfish, however, periods of lethal exposure to fresh water are too long to be practical.

Since death in fresh water is the result of upsetting the isotonic balance between body fluids of the organism and its environment (Prosser et al. 1950, and many others), it was suspected that death

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could be achieved much more rapidly in waters of greatly increased salinity. In a highly hypertonic solution, an aquatic animal's body fluids might be lost resulting eventually in destruction of cells and organs.

Loosanoff (1957) conducted experiments in which he killed several oyster enemies by exposing them to saturated salt solutions (300 parts per thousand) for certain periods followed by drying them in air (Table 1). The present study was undertaken to determine the effects of less than saturated salt solutions on these enemies.

METHODS

In these experiments a saturated solution of "rock salt" was prepared and then diluted with sea water to give 90, 80, 70, 60, 50, 40 and 30 per cent saturated solutions.

Because it had previously been found that oyster enemies were killed within 15 minutes in a saturated salt solution (Table 1), the periods employed in this study were 1, 3, 5, 10 and 15 minutes.

Table 1. Minimum exposures in a saturated salt solution and drying times required to cause 100 per cent mortality of six species of oyster enemies (Loosanoff 1957).

	Exposure in minutes	Drying time in minutes						
		None	5	10	15	30	45	60
Asterias forbesi	3	X						
Molgula manhattensis	5-10	X						
Cliona celata	3-5							X
Crepidula fornicata	5				X			
Urosalpinx cinerea and *Eupleura caudata* egg cases	5	X						

Drying, which prolongs the contact of animals with salt and concentrates unsaturated solutions by water evaporation, was used only where it had proven necessary before. Starfish and drills were kept for 14 days in running sea water in the laboratory following salt treatments. Other animals were suspended for the same period in Milford Harbor in perforated plastic boxes which allowed adequate circulation of water.

RESULTS

Boring Sponges

Two samples of ten marketable-sized oysters infested with *Cliona celata* were exposed to salt solutions for each immersion period. One sample from each was dried for one hour. Drying caused much higher mortalities (Tables 2 and 3).

Sponges, extended with their oscula open in normal sea water, contracted during exposure. Dying and decomposing sponges pass through several color changes. From a deep, rich yellow they change to tan, black and then to white.

Starfish

All starfish (10 per sample) were killed by an exposure of one minute in 100, 90, 80 and 70 per cent saturated solutions. In 60 and 50 per cent saturated solutions three-minute exposures killed them. Starfish were not killed when exposed 15 minutes in solutions less than 50 per cent saturated. Water temperatures during this experiment ranged between 13 and 17.2°C.

During the drying periods, red pigment was observed to leach slowly from the starfish's integument. If starfish were placed in normal sea water immediately following exposure, much red pigment was lost from their ruptured body cells and organs, and their rays shrank and curled at the tips. Soon the starfish flattened out, and autotomy of the rays and rapid disintegration of the animal followed.

Tunicates

Twenty-five unattached *Molgula manhattensis* were used in each sample. Salt solutions 100 and 90 per cent saturated killed tunicates within five minutes. Solutions 80, 70 and 60 per cent saturated killed them within ten minutes and 50 and 40 per cent saturated solutions, within 15 minutes (Table 4).

Dead tunicates usually remained rigid for several days after their return to sea water, but then became flabby and often eviscerated themselves.

Table 2. Per cent mortalities of sponges 14 days after their exposure to salt solutions of different strengths and immediate return to sea water. Sea water temperature 9 - 11°C

Immersion in minutes	Per cent saturation							
	100	90	80	70	60	50	40	30
1	0	0	*	0	0	0	0	0
3	10	0	*	0	0	0	0	0
5	100	50	50	0	20	0	0	0
10	100	100	90	100	100	50	0	0
15	100	100	100	100	100	0	0	0

*Sample lost

Table 3. Per cent mortalities of sponges 14 days after their exposure to salt solutions of different strengths and drying for one hour. Sea water temperature 9 - 11°C

Immersion in minutes	Per cent saturation							
	100	90	80	70	60	50	40	30
1	100	100	50	60	75	25	0	0
3	100	100	100	80	100	80	0	0
5	100	100	100	90	50	50	0	0
10	100	100	100	100	100	50	25	0
15	100	100	100	100	100	100	50	0

Table 4. Per cent mortalities of tunicates 14 days after exposure to salt solutions of different strengths. Sea water temperature 5.2 - 11.5°C

Immersion in minutes	Per cent saturation							
	100	90	80	70	60	50	40	30
1	8	12	8	8	16	4	0	0
3	72	40	20	52	24	4	8	8
5	100	100	64	84	20	12	12	0
10	100	100	100	100	100	96	80	4
15	100	100	100	100	100	100	100	0

Drills

Urosalpinx cinerea is an extremely hardy animal capable of isolating itself from unfavorable environmental conditions by tightly closing its operculum (Carriker 1955). Therefore, it was decided to try a saturated solution for periods as long as 30 minutes, one hour and three hours before proceeding to weaker solutions and shorter exposures. Groups of 50 drills were exposed to these conditions. Following exposures to salt solutions one-half the drills in each group were returned to normal sea water and the others were dried for one hour. Only three of the six treatments caused any mortality. Eight per cent of the drills died after three hours of exposure and immediate return to sea water; 12 per cent died after one hour of exposure and one hour of drying; and 32 per cent died following three hours of exposure and one hour of drying.

Although drills are not readily killed by this method, it was found to be quite successful in killing embryos of U. cinerea and Eupleura caudata, regardless of their stage of development (Table 1).

Oysters

Eight to 15 Crassostrea virginica, 10 to 20 millimeters in length, were used in each sample. Few oysters died after exposure to any salt treatment, provided the edges of their thin shells were not chipped (Table 5). Chipped oysters were killed. While exposed to salt solutions, oysters remained tightly closed, except when they opened their shells slightly, probably to test the water. There was evidence that oysters were adversely affected by salt solutions because some of them did not produce true feces for several days follow-

ing a treatment; however, all produced pseudofeces.

Table 5. Per cent mortalities of young oysters, 10 to 20 millimeters in length, 14 days after exposure to salt solutions of different strengths. Sea water temperature 9 - 11°C

Immersion in minutes	Per cent saturation							
	100	90	80	70	60	50	40	30
1	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
3	2.1	11.1	3.0	0.0	0.0	0.0	0.0	0.0
5	0.0	10.2	0.0	0.0	0.0	0.0	3.1	4.0
10	4.3	3.5	0.0	9.0	2.3	0.0	1.8	0.0
15	0.0	3.3	*	0.0	0.0	0.0	0.0	0.0

*Sample lost

DISCUSSION

Several oyster enemies can be killed readily by exposing them to partially saturated salt solutions. Effective concentrations can be easily maintained by constantly stirring salt crystals into solution.

In practice, if several enemies are involved, the salt treatment should be administered to kill the species most resistant to it.

Since water temperatures during these experiments ranged from 5 to 17.2°C, repetitions of them are planned for water temperatures ranging between 15 and 25°C. At higher temperatures, minimum exposures for these enemies may be considerably shorter.

ACKNOWLEDGMENTS

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A High School Oceanographic Laboratory

By

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A High School Oceanographic Laboratory

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Introduction

Recently much attention has been focused on the study of oceanography. The first International Oceanographic Congress was held in August, 1959 at the United Nations Building in New York. Approximately 1000 delegates representing 54 nations participated. The National Academy of Sciences recently released its report concerning the great necessity for expanding ocean research. Both of these events received coverage in press releases resulting in numerous newspaper and magazine articles reaching a large part of the world population.

Oceanography is a new frontier of science which will challenge the imagination of any alert student. Problems concerning almost every basic biological and physical concept are present. Here is an environment that presents a great opportunity for original investigation. The physiology, morphology, and ecology of only a small number of marine organisms is now generally understood, particularly those which have little or no commercial importance. There are many gaps in our knowledge concerning the physical properties and biological populations of the world's oceans. An oceanographic laboratory will afford participating students in coastal communities a unique opportunity to become familiar with research methods and problem solving techniques. There is also good indication that a number of these students could conceivably contribute to a better understanding of man's newest frontier, the oceans.

Organization

The methods of organizing a laboratory are varied depending largely upon local conditions. Initially one should probably begin with a small group of students possessing high aptitudes and a genuine curiosity concerning the oceans.

Selection at Randolph High School, Randolph, Massachusetts, was on a competitive basis. Five classes of sophomore biology students were given two lessons concerning the cycle of life in the oceans with particular emphasis on its origin, economic importance, physical features, and untapped resources. The students were then required to complete a report of approximately 1500 words entitled, "The Cycle of Life in the Oceans," using a minimum of three reference books. Students who produced the most comprehensive reports were later interviewed, and from this group ten who showed a genuine curiosity, interest, and aptitude were selected to become staff members of the laboratory.

The students selected were encouraged to familiarize themselves with oceanographic literature which was made available. They discussed their findings at a meeting, at which time it was generally held that while there were a great many excellent problems to work on, many were impractical from the standpoint of available equipment, time, and the difficulty of securing adequate samples. It was decided to begin the studies with readily available local fish species which not only provided interesting problems but also the opportunity to secure valuable scientific data.

Equipment

The high school biology laboratory is an ideal place to center student activity after regularly scheduled classes. Available in most laboratories are work benches, running water, electrical outlets, cabinets, blackboards, and the essential equipment listed below. Very little special equipment need be purchased.

The following list of items were used by students at Randolph High School. Unless otherwise indicated the equipment was available for use in the regularly scheduled biology laboratory sessions.

1. Library
   a. A number of periodicals, scientific reprints and textbooks were purchased or otherwise acquired to provide easy access for essential background literature. See general reference section.

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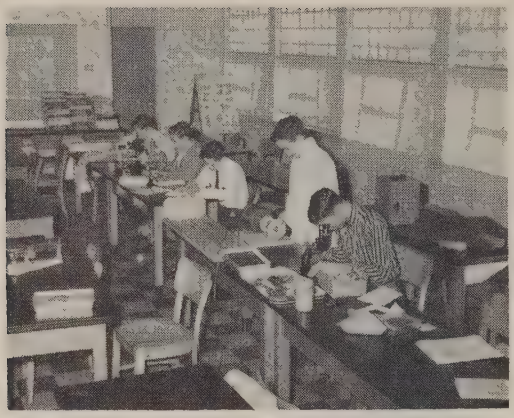

Figure 1. Several members of the Randolph High School Oceanographic Laboratory Staff at work: (left to right) Fred Hubble and Robert Merritt are examining plankton collected for their productivity studies. George Fahey is busy checking through the literature concerning the distribution of the tomcod, while Peter McGrath is shown grinding down a bone (otolith) taken from the skull in an effort to observe the growth pattern of annual rings similar to those found in a tree. Everett Schaner is examining the gonads as part of his fecundity study of the same fish.

b. Arrangements were made with the Library of the Museum of Comparative Zoology at Harvard to use its reference collection.
c. The laboratory was put on the mailing list for receiving fishery research papers published by the U. S. Bureau of Commercial Fisheries.
d. A catalogue listing available scientific reprints in the laboratory was compiled by students.

2. Audio-visual equipment
   a. 16mm. sound motion picture projector. Excellent motion pictures concerning oceanographic research are available on loan from the University of Miami Marine Laboratory. The U. S. Bureau of Commercial Fisheries also has films available on loan from large university audio-visual centers.
   b. Slide projector
   c. Tape recorder
3. Microscopes
   a. Ten monocular student type with two objectives 10x and 40x.
   b. Five binocular dissecting type with interchangeable eye pieces, of 10x, 20x, and 30x.
   c. Ten microscope lamps.
   d. Microprojector.
4. Dissecting equipment
   a. Thirty dissecting kits containing scalpel with changeable blades, two probes, forceps, scissors, ten cm. rule, and dissecting pins.
   b. Thirty wax bottom dissecting pans.
   c. Three large filleting knives (special purchase).
   d. Two sets of metal tongs for handling preserved specimens.
5. Measuring devices
   a. Three balance scales, maximum weight—150 grams.
   b. Three meter sticks.
   c. One 36 cm. fish measuring board (special construction).
   d. One analytical balance.
   e. One set of calipers, scale 10 cm. in 1 mm. divisions (special purchase).
   f. Thermometer—measuring water temperature.
   g. The laboratory members were allowed use of an analytical balance at the Quincy City Hospital for precise measurements during one of the fecundity studies.
6. Collecting gear
   a. Two fine mesh plankton nets (special purchase).
   b. Fishing lines and assorted tackle (special purchase).
   c. Three metal barrels for storing specimens; refuse type available with covers at most hardware dealers (special purchase).
   d. Ten dozen assorted jars for preserving specimens (special purchase).
   e. Four canvas water buckets (special purchase).
   f. Two small seines (special purchase).
   g. Fish tags and tagging gear were kindly provided on loan from the U. S. Fish and Wildlife Service, Woods Hole, Massachusetts.
   h. Many specimens were collected from cooperative fishermen in the ports of Boston, Hull, and Cohasset.
7. Vessels
   a. The laboratory was allowed the use of a 16 ft., 18 h.p. Thompson runabout which was available for sampling trips.
   b. A number of sampling trips were taken from small rented outboard boats available at various ports along the coast at a cost of approximately two dollars an hour. The expense of renting a vessel was shared equally among the staff members.

Figure 2. Peter McGrath weighing a tomcod as part of his age and growth study.

8. Preserving materials
   a. 15 gallons of formaldehyde for specimens (special purchase).
   b. 5 gallons of isopropyl alcohol for specimens (special purchase).
      Note: Most specimens can be hardened in 10% formalin and then preserved in 30% isopropyl alcohol.
   c. Large ice-cream freezer for freezing and storage of specimens (on loan from local dairy).
9. Chemical supplies (available on loan from chemistry department).
10. Physical science apparatus (available on loan from physics department).
11. Office supplies including typewriters and duplicating materials (available from school business training department).
12. Woodworking supplies (available from woodworking department).
13. Heavy machinery (limited supply available from school auto-shop department).

Selection of Projects

The selection of research projects depends largely on availability of equipment, time, the opportunity for adequate sampling of organisms, and environmental variables.

Numerous projects worthy of short term investigations are present in the nearshore marine environment. The following list contains titles and brief descriptions of projects initiated by students at Randolph High School. Also included are some suggested projects for study. One need only to browse through the many scientific periodicals concerned with marine investigations to realize the varied research now in progress involving the biology, chemistry, and physics of the oceans. The following list is far from complete and only suggestive of the myriad of ocean problems suitable for high school research.

Figure 3. Everett Schaner removing the ovaries of a ripe female tomcod. Later he will determine the total number of eggs contained by this individual as part of his fecundity study.

Figure 4. Fred Hubble and Robert Merritt examine samples of plankton taken from surface tows off the coast of Hull Bay, Massachusetts. George Fahey is busy checking the feeding habits of the tomcod for possible correlation with the plankton productivity investigation.

Problems under Investigation at Randolph High School

1. Fishes
   a. Observations on the fecundity of the Tomcod, *Microgadus tomcod* (Walbaum)
      Investigator—Everett Schaner (sophomore)
      Description—Analysis of ovaries taken from 100 Tomcod for fecundity estimate; requiring weighing of a specified number of ova, relating this value to total ovary weight on a seasonal basis including ova, ovary, and fish measurements showing seasonal increase in size until spawning. Average numbers of ova in mature female gave an approximation of Tomcod fecundity.
      Reference: Yuen, H. S. H.
      Maturity and fecundity of bigeye tuna in the Pacific. 1955. U. S. Fish and Wildlife Service, Special Scientific Rept. Fisheries No. 150, 30 pp.
   b. Food habits of the Tomcod *Microgadus tomcod* (Walbaum)
      Investigators—Mary Landry and Nancy Lehtinen (sophomores)
      Description—Stomachs from 50 Tomcod were examined for stomach contents noting the numbers and weight of organisms present, identified to phylum and order, to determine the trophic level utilized by the Tomcod. This information was analyzed with respect to available data concerning Tomcod ecology and abundance.
      Reference: Jensen, A. C., and R. L. Fritz
      Observations on the stomach contents of the silver hake. 1960. Transactions. Amer. Fish. Society, Vol. 89, No. 2, pp. 239-240.

c. Observations on the age and growth of the Tomcod, *Microgadus tomcod* (Walbaum)
Investigator—Peter McGrath (sophomore)
Description—Otoliths, small arrow shaped bones suspended in a watery sinus in the skull, from 50 Tomcod of various sizes were removed and examined to determine their usefulness as indicators of fish age. Annual rings were counted and compared with fish length. In this way an age approximation and growth curve were estimated.
Reference: Lux, F. E.
Age determination of fishes. 1959. U. S. Fish and Wildlife Service. Fishery Leaflet No. 488, 10 pp.

d. Observation of the age and growth of the Longhorn Sculpin, *Myoxocephalus octodecimspinosus* (Mitchill)
Investigator—Gene Cohen (sophomore)
Description—Otoliths were removed from 25 fish of different size groups. Annual rings were counted and compared with fish length to approximate fish age and rate of growth.
Reference: Morrow, J. E., Jr.
The biology of the Longhorn Sculpin, Myoxocephalus octodecimspinosus, *with a discussion of the southern New England "trash" fishery.* 1951. Bulletin of the Bingham Ocean. Coll. Vol. 13, No. 2, 89 pp.

2. Plankton

a. Observations of the nearshore zooplankton fauna collected from Cohasset, Massachusetts
Investigator—Robert Merritt (sophomore)
Description—Zooplankton organisms were collected during the winter months with a fine mesh nylon plankton net using both vertical and horizontal tows of approximately ten minutes' duration. Zooplankters were classified by major groups. An estimation was made of the relative percentage of group composition.
Reference: Deevy, Georgiana B.
Oceanography of Long Island Sound. Part V, Zooplankton. 1956. Bulletin of the Bingham Ocean. Coll. Yale Univ., Vol. 15, pp. 113-155.

b. Observations of the nearshore phytoplankton fauna collected from Cohasset, Massachusetts
Investigator—Fred Hubble (sophomore)
Description—A number of large diatoms were removed from the same plankton collections used by R. Merritt (see above). They were classified by groups. An estimate was made of the percentage composition of each group.
Reference: Conover, Shirley, A. M.
Oceanography of Long Island Sound. Part IV, Phytoplankton. 1956. Bulletin of the Bingham Ocean. Coll. Yale Univ., Vol. 15, pp. 62-112.

Suggested General Problems for Investigation

The following list contains a few suggested problems in each of the three major areas of oceanographic research and includes recent references useful for organizing the investigation.

1. Biological oceanography

a. Follow the distribution pattern in both space and time of a marine organism, fish or invertebrate. This will require the marking of a large number of organisms using tags or other means in order to accurately determine migration patterns and growth rates.
Rounsefell, G. A., and J. L. Kask.
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Data Collection

Perhaps the most important aspect of any research endeavor is the collection of information regarding the various stages of project development referred to as data.

To assure adequate recording of this data it is important to outline the project carefully considering the data to be collected in order to achieve successful results. Mimeographed forms are most useful since in most instances a good deal of replicate type data is needed in oceanographic research. The type of information to be recorded will of course vary greatly with each project. However, in most instances the mimeograph data sheet should contain a few essentials such as project title, date, signature of individual collecting data, and a method of numbering observations.

Reporting Project Results

Investigation results should be presented in a form suitable for publication in appropriate

scientific periodicals. For the most part the projects under consideration at the high school level will be short term investigations which could be prepared as brief observations and scientific notes. Included below is a partial listing of scientific periodicals which will accept for publication short manuscripts containing significant scientific contributions.

1. *Copeia*, published quarterly by the American Society of Ichthyologists and Herpetologists.
   Managing Editor—
   Dr. David L. Jameson,
   Dept. of Biology,
   San Diego State College,
   San Diego, California.
2. *Journal of the Fisheries Research Board of Canada*, published bi-monthly by the Fisheries Research Board of Canada.
   Editor—
   Dr. W. E. Ricker,
   Fisheries Research Board of Canada,
   P.O. Drawer 100,
   Nanaimo, British Columbia,
   Canada.
3. *Journal of Marine Research*, published by the Sears Foundation for Marine Research, Bingham Oceanographic Laboratory, Yale University.
   Managing Editor—
   Yngve Olsen,
   Bingham Oceanographic Laboratory,
   Yale University,
   New Haven, Connecticut.
4. *Limnology and Oceanography*, published quarterly by the American Society of Limnology and Oceanography.
   Editor—
   Dr. K. M. Rae,
   Dept. of Oceanography and Meteorology,
   A and M College of Texas,
   College Station, Texas.
5. *The Biological Bulletin*, published by the Marine Biological Laboratory, Woods Hole, Massachusetts (will accept only comprehensive studies for publication).
   Managing Editor—
   Dr. Donald P. Costello,
   P.O. Box 429,
   Chapel Hill,
   North Carolina.
   From June 1 to Sept 1 manuscripts should be sent to Managing Editor, Marine Biol. Lab. Woods Hole, Mass.
6. *Transactions of the American Fisheries Society*, published quarterly by the American Fisheries Society.
   Editor—
   Dr. L. L. Smith, Jr.,
   300 Coffey Hall,
   University Farm,
   St. Paul 1, Minnesota.

Scientific publications for the secondary school:

1. *Science World Magazine*, published bi-weekly from September to June.
   Editor—
   Dr. Eric Berger,
   33 West 42nd St.,
   New York 36, New York.
2. *Megalops*, to be published semiannually by the Randolph High School Oceanographic Laboratory. Address Student Managing Editor—
   Mr. Everett Schaner,
   Randolph High School,
   Oceanographic Laboratory,
   Randolph, Massachusetts.

The manuscript should be typed double space on standard 8½″ by 11″ good grade bond paper. Accompanying figures and tables should appear on separate sheets. Figures should be drawn in India ink on good grade drafting paper. Most all periodicals contain specific instructions pertaining to manuscript preparation and should be consulted. Familiarization with the style used in the periodical selected is essential.

Generally the following headings should be used.

1. Introduction
2. Methods and Materials
3. Results
4. Discussion
5. Conclusions

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OCCURRENCE OF EARLY DEVELOPMENTAL STAGES OF THE OBLONG OCEAN SUNFISH *RANZANIA LAEVIS* (PENNANT) IN THE CENTRAL NORTH PACIFIC.—Little has been reported concerning the morphology and distribution of the early developmental stages of the oblong ocean sunfish, *Ranzania laevis* (Pennant), in the central North Pacific. The only previous report is that of Jordan and Snyder (1901, *Proc. U. S. Nat. Mus. 24(1254):263*), who mention a 4-inch specimen (referred to as *R. makua*) collected at Honolulu but offer no additional information. Mention of adult oblong ocean sunfish occurrences in the central North Pacific, usually of single specimens collected from the immediate vicinity of Honolulu, are more numerous: Jenkins (1895, *Proc. Calif. Acad. Sci. 5:779–84*), reported a new species, *R. makua* Jenkins, collected from the vicinity of Pearl Harbor, Oahu; Fowler (1900, *Proc. Acad. Nat. Sci. Phila:514*), described a skin of *R. makua* collected by J. K. Townsend in Honolulu in 1835; Jordan and Evermann (1903, *Bull. U. S. Fish Comm. 23:440*), provided a redescription of the type specimen, *R. makua*; Gunther (1910, *J. Mus. Godeffroy 9(17):477*), reported a specimen of *R. truncata* collected from the Hawaiian Islands; Jordan and Jordan (1922, *Mem. Carnegie Mus. 10(1):89*), mention four *R. makua* collected from Honolulu; Fowler (1922, *Copeia 112:84*), listed *R. truncata* as present in the fish collection of the *Acad. Nat. Sci. Phila.*; Jordan, Evermann and Tanaka (1927, *Proc. Calif. Acad. Sci. 16(4): 680*), include *R. makua* in a list of fishes collected from the Hawaiian Islands; Fowler (1928, *Mem. Bishop Mus. 10:475*), reported the collection of single specimens of *R. truncata* on several occasions at Honolulu and later (1938, *Acad. Nat. Sci. Phila. Mon.*) included *R. truncata* in a list of fishes collected from Eastern Oceania.

This report is concerned with the morphology and distribution of early developmental stages of *R. laevis* from plankton samples in the collections of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii (HBL).

A total of 1,531 identifiable young stages of *R. laevis* were separated from 98 plankton samples, of which 28 contained specimens, (Table 1). These plankton samples had been collected during 1959 as part of an oceanographic survey of Hawaiian waters, extending from 13° to 26°N. latitude and from 145° to 170° W. longitude (Fig. 1). All hauls were of 30 minutes duration and were taken at approximately 2100 hours using a 1-m net (aperture widths: belly section, 0.65 mm; rear section 0.3 mm) towed obliquely from 60 m to the surface, with the exception of two oblique tows from 140 m. An additional 1,084 *R. laevis* larvae were separated from plankton samples collected from an International Geophysical Year monitoring station located at 21°10′N. latitude, 158°19′W. longitude. The station was occupied at monthly intervals from July to December 1958 by HBL personnel. When conditions permitted, two evening and two daylight oblique tows from 60 m to the surface were taken with a 1-m net (aperture widths same as above). Of a total of 64 samples collected, only

TABLE 1. SEASONAL OCCURRENCE OF *Ranzania laevis* COLLECTED IN 1959 ON OCEANOGRAPHIC SURVEYS, 13° TO 26°N., 145° TO 170°W.

	Jan.–Feb.	March–April	May	July	Oct.
Number of plankton hauls	31	21	22	13	11
Number of hauls containing *R. laevis*	13	12	3	—	—
Total number of *R. laevis*	852	671	8	—	—

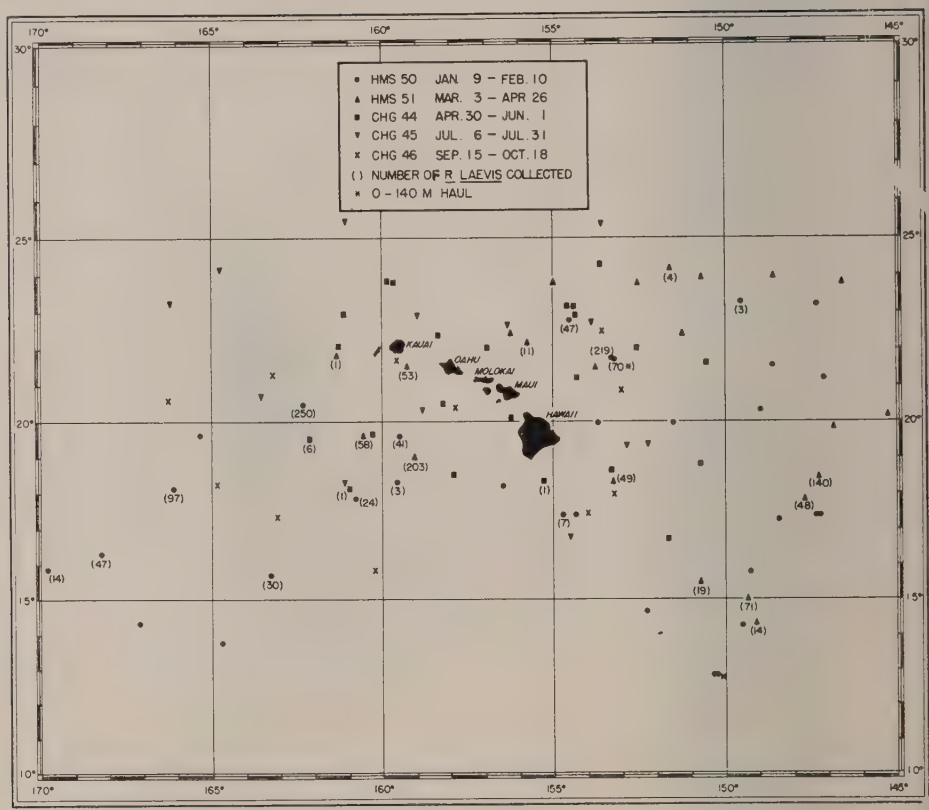

Fig. 1. Cruise periods, vessel positions during plankton hauls, and positions of larval occurrence of *Ranzania laevis*. HMS = *Hugh M. Smith*, CHG = *Charles H. Gilbert*.

Table 2. Seasonal and Day-Night Variation in Numbers of *R. laevis* Collected in 1957–58 from the IGY Plankton Station, 21°10′N., 158°19′W.

Date	Number of daylight tows	Number of *R. laevis*	Number of night tows	Number of *R. laevis*	Vessel and cruise
7/21/57	1	—	1	—	Charles H. Gilbert—34
8/20/57	1	—	2	—	" " " "
9/16/57	2	—	2	—	Hugh M. Smith—41
10/29/57	2	—	2	—	" " " "
11/26/57	2	—	2	—	" " " —42
12/19/57	2	—	2	—	Charles H. Gilbert—36
1/21/58	2	759	2	252	" " " —37
2/27/58	2	65	2	8	Hugh M. Smith—43
3/24/58	2	—	2	—	" " " —44
4/21/58	1	—	2	—	Makua—13
5/30/58	2	—	—	—	Charles H. Gilbert—39
6/21/58	2	—	2	—	" " " "
7/21/58	—	—	2	—	Hugh M. Smith—46
8/19/58	2	—	2	—	Charles H. Gilbert—41
9/25/58	2	—	2	—	" " " "
10/21/58	2	—	2	—	Makua—14
11/20/58	2	—	2	—	Hugh M. Smith—48
12/18/58	2	—	2	—	" " " —49
Total	31	824	33	260	

four contained *R. laevis* larvae (Table 2). In addition to the specimens found in the plankton samples, I examined nine juvenile *R. laevis* (12–82.5 mm T.L.) which were washed up at Maili, Oahu, where they were collected by Mr. K. Ego of the Hawaii Division of Fish and Game, during May 1959; and an adult female (335 mm T.L.) specimen collected from the stomach of

TABLE 3. SUMMARY OF DATA ON THE ONTOGENY OF *Ranzania laevis*

Panel A.—Selected morphological characters of *R. laevis* collected from the central North Pacific compared with the description of *R. laevis* larvae from the Sargasso Sea.

	Present study	Schmidt 1932 Fig. 197
Egg length in mm.	—	1.3–1.4
First larva		
Total length in mm	1.5–1.7	1.7
Spines	absent	absent
Caudal region	well developed	well developed
Second larva		
Early stage		
Total length in mm	1.8–2.2	1.8–2.4
Paired spines	7[1]	—
Unpaired spines	6	—
Caudal region	beginning to atrophy	beginning to atrophy
Middle stage		
Total length in mm	2.3–4.5	2.4–3.5
Paired spines	7	—
Unpaired spines	6	—
Caudal region	atrophying	atrophying
Late stage		
Total length in mm	4.6–8.0	8.0
Spines	diminishing in number and size	diminishing in number and size
Caudal region	greatly reduced	greatly reduced
Caudal fin	absent	absent

Panel B.—Morphometric and meristic data on juvenile *R. laevis* from Hawaiian waters

	Total length (snout to outer margin of caudal fin)	Fin ray counts				Vertebral count	Depth measured bisecting pectoral	depth/length
		P	D	A	C			
	mm.						*mm.*	
Early stage	12.0	13	18	18	21	—	8.5	.71
	14.2	13	18	18	20	—	8.5	.60
	18.5	13	18	18	20	—	10.0	.54
	23.0	13	18	18	21	—	10.5	.46
Late stage[2]	62.6	13	18	19	21	—	18.0	.29
	69.8	13	18	19	21	—	17.0	.24
	76.0	13	17	19	21	8 + 10	19.1	.25
	77.4	13	18	19	21	8 + 10	20.0	.26
	82.5	13	18	19	19	—	21.0	.25

Panel C.—Vertebral counts and depth/length relations of adult *R. laevis* from Hawaiian waters and specimen described from the Atlantic

	Total length (snout to outer margin of caudal fin)	Standard length	Fin ray counts				Vertebral count	Depth measured bisecting pectoral	depth/length
			P	D	A	C			
	mm.	*mm.*						*mm.*	
Adult[3]	335	321	13	damaged			8 + 10	121	.36 or .38[4]
Hasler-Brunner 1951 94	—	—	—	—			8 + 10 or 11	—	< .50

[1] An additional pair of poorly developed spines is present above orbit.
[2] Washed up on Maili Beach, Oahu.
[3] Found in stomach of marlin, *Makaira* sp., examined at United Fish Market, Oahu, 10/13/60.
[4] Using total length or standard length, respectively.

a marlin, *Makaira* sp., at the United Fish Market, Honolulu, on October 10, 1959.

According to Fraser-Brunner (1951, *Bull. British Mus. Nat. Hist. 1(6):96*), two subspecies of *R. laevis* can be recognized: *R. l. makua* Jenkins in the Pacific and *R. l. laevis* (Pennant) in the Atlantic. Major adult morphological features discussed by Fraser-Brunner are carapace depth and the position of the pectoral fin axil. For *R. l. makua* he reports that carapace depth is greater than half the length, and the axil is located above the center of the eye. In *R. l. laevis* carapace depth is reported less than half the length, and the pectoral fin axil is located below the center of the eye. The adult specimen collected during the present study agreed on these points with the description of *R. l. laevis* given by Fraser-Brunner (Table 3, panel C).

The developmental stages of *R. laevis* found in the plankton samples were compared to the descriptions by Schmidt (1932, *Dana's Togt omkring Jorden: 250–5*) and Tortonese (1956, *Fauna e Flora del Golfo di Napoli, Monog. 38: 965–71*). Excellent agreement was found between the lengths and changes in form of the caudal region at various larval stages as given by Schmidt (*ibid.*, fig. 197) and as seen in my specimens (table 3, panel A). The number of spines, seven paired and six unpaired, found in specimens measuring 2.3–4.5 mm was in agreement with the number found by Tortonese (*ibid.*, 970) in a 2.8-mm specimen collected from the Strait of Messina.

Perhaps some of the confusion found in the literature regarding the nomenclature of *R. laevis* is attributable to the marked changes in form which are characteristic of this fish. The number of pectoral fin rays (13) and the vertebral count (8 + 10) of the juvenile *R. laevis* collected from the beach at Maili, Oahu, are in agreement with corresponding counts given by Fraser-Brunner for adult specimens. However, the depth/length ratio of these juvenile specimens (Table 3, panel B) varies from 0.71 in a 12-mm (T.L.) specimen to 0.25 in an 82.5-mm individual, indicating a change in body form with increase in length. Carapace depth in the older specimens of *R. laevis* is less than half the length, as evidenced from the 335 mm adult collected during the present study, in which the depth/length ratio was found to be <0.50 (Table 3, panel C). Although only one adult was examined, the resulting measurements, when considered with the similarity in larval development between Atlantic specimens and the present series of Pacific specimens, suggest that *R. laevis* is distributed in both Atlantic and Pacific waters.

The only definite record regarding spawning grounds of *R. laevis* is that of Schmidt (1921, *Nature, Lond. 107:76–79*), who reported that viable *R. laevis* eggs (referred to as *R. truncata*) were collected from depths of approximately 100 m in the Sargasso Sea and hatched aboard the *Dana*. In the present study *R. laevis* larvae were collected in varying numbers throughout the entire survey region with no apparent concentration in any one sector (fig. 1). The greatest numbers of *R. laevis* were found in plankton samples collected during late winter and early spring (table 1) in the oceanographic survey series, and during January and February in the IGY collections (table 2). Considerably greater numbers of *R. laevis* were found in the daylight than in the night samples. Abundance of *R. laevis* in all stages of larval development from January to April indicated that considerable spawning had occurred. Absence of appreciable numbers of larval stages during other months of sampling suggests that *R. laevis* spawns only during the late winter and early spring in the Hawaiian region.

In this connection it is noted that the adult ♀ *R. laevis* collected at the United Fish Market, Oahu, in October 1960 contained a large number of developing opaque yellowish ova measuring 0.5 mm. in diameter.

Whether the juvenile *R. laevis* washed up at Maili, Oahu, were members of the 1959 year-class is open to speculation in the absence of adequate growth data.

I am indebted to Messrs. Gary Miller and Edward Kamaura of the HBL for their assistance in the tedious work of separating *R. laevis* from other plankton constituents, and also to Mr. Wilvan G. Van Campen of the HBL staff for his translation of pertinent passages in Danish and Italian publications.—KENNETH SHERMAN, *United States Department of the Interior, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.*

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INCIDENCE OF THE COD PARASITE *LERNAEOCERA BRANCHIALIS* L. IN THE NEW ENGLAND AREA, AND ITS POSSIBLE USE AS AN INDICATOR OF COD POPULATIONS

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Bureau of Commercial Fisheries, Woods Hole, Massachusetts

ABSTRACT

A total of 4,519 cod, *Gadus morhua* L., from the coastal and offshore regions of New England were examined during June to December 1957 for the parasitic copepod, *Lernaeocera branchialis* L. Infestation decreased from north to south and inshore to offshore.

The effect of infestation on the length–weight relationship of cod was examined and found non-significant. An examination of infestation selectivity by fish size also showed no significant differences.

From the differential infestation rates, it is shown that four general groups of cod can be distinguished: those of the northern Gulf of Maine heavily infested, the moderately infested central and southern Gulf cod, the lightly infested Georges Bank population, and the southern New England group which is free of infestation. This supports previous unpublished tag return data, and indicates the usefulness of *Lernaeocera* for distinguishing various groups of cod.

INTRODUCTION

Investigators of the problem of group differences within fish species, employing methods such as meristic counts, age and growth comparisons, morphometric studies and tagging have been able to separate and identify some lesser divisions (Marr 1957). Serological studies (Cushing 1952), physiological determinations (Farris 1957) and uses of naturally occurring parasites as biological tags (Sindermann 1957; International North Pacific Fisheries Commission 1956) have also been utilized with varying degrees of success.

For several years, scientists of the Fisheries Research Board of Canada have been collecting data on the infestation of cod, *Gadus morhua* L., by the copepod parasite *Lernaeocera branchialis* L. Templeman (1953) reported differential infestation rates, low in the offshore region of Newfoundland and relatively high in the southeastern inshore area.

The purpose of the present study was to determine whether differential infestation rates also exist in New England waters. An attempt was made to determine the effect of infestation upon the condition of the fish and to establish a relationship between the size of cod and infestation rate. A limited amount of pertinent life history data concerning *Lernaeocera* was also collected.

The area chosen for study includes most of the New England coastal region and adjoining offshore banks, extending northward from Pt. Judith, Rhode Island, to the Islands of Campobello and Grand Manan, New Brunswick. This area had previously been divided into statistical subareas by the North American Council on Fishery Investigations (Rounsefell 1948). These subareas were used as basic units of study, treating the fish taken from each of them independently (Fig. 1).

METHODS

From June until December 1957, a total of 4,519 cod were examined in the New England area for incidence of *Lernaeocera*.[1] Sampling was opportunistic because of the

[1] A. G. Humes of Boston University confirmed our identification of the parasite.

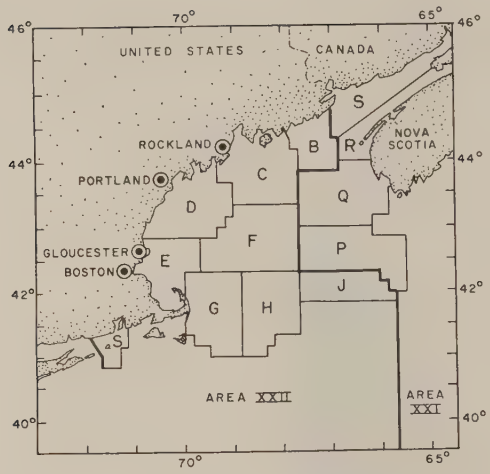

Fig. 1. Statistical subareas discussed in text (after Rounsefell, 1948).

normal vagaries of the fishery and the weather, but an attempt was made, wherever possible, to obtain samples from each of the various market size categories of cod landed and from the different fishing areas. Generally, these objectives were achieved with the exception of the largest size category. These were scarce in the commercial catch and when present, were usually beheaded, making it impossible to ascertain the presence or absence of the parasites.

The method of sampling varied slightly according to conditions but ideally all of the infested and non-infested cod were measured to the nearest millimeter (fork length) and weighed to the nearest ounce. Examination of cod for the presence of the adult parasite is simple due to the nature of the organism, which is large (ranging from 1.5 to 2.6 cm in length with the average about 2.3 cm) and blood-red. It may easily be seen attached to the isthmus of the gills when the fish is placed on its dorsal side with the opercles spread.

Most of the fish were examined at the dockside after they were unloaded from commercial vessels. The validity of this method was checked on one or two occasions by sampling the same vessel's catch at sea and in port. Sometimes softer body parts of the parasite were crushed, but this did not affect results since the elongated chitinous "neck" remained imbedded and could easily be detected either by visual examination or by running thumb and forefinger along the isthmus.

Circulars were sent to fish dealers and bait-shop operators in an effort to secure specimens of *Lernaeocera* from a wide variety of environments in New England. As a fortunate result, an immature "Pennella" stage not previously recorded from the Western Atlantic was found attached to a 32-cm cod caught south-southwest of Plymouth, Massachusetts, in 30 ft of water.

A. M. Fleming (personal communication) of the Fisheries Research Board of Canada has found larval stages on the gills of the lumpfish (*Cyclopterus lumpus*), indicating that in Canadian waters as in Europe this fish is an intermediate host. The gills of 30 lumpfish from various parts of the Gulf of Maine area were examined in the laboratory during the present investigation. Of these, 6 from the inshore Eastport area were infested with larval *Lernaeocera*.

RATES OF INFESTATION

Details of the life history of *L. branchialis* are to be found in Scott (1901), Sproston (1942), Capart (1947, 1948) and Dollfus (1953). It is probable that the adult female stays on the definitive host for a period of years. A survey of the literature indicates that it has a boreo-arctic distribution in the Atlantic which parallels the distribution of *Gadus* spp. in all areas excepting the southerly sections of the coastlines of Spain and the United States. In these areas, cod penetrate farther south than *Lernaeocera*, indicating some limiting factor for the latter. The distribution of some intermediate host(s) might be suggested as a possibility.

In the following discussion of the samples collected, notes explain the sampling conditions and peculiarities of the fishery in each subarea as they affect the samples. Fish sizes are defined as: Small, 0–50 cm; Medium, 51–75 cm; Large, 76–100 cm; and Extra Large, 101 cm and over. These correspond rather closely to the market categories used in some areas: Scrod, 1½ to 2½ lb;

Market, 2½ to 10 lb; Large, 10 to 25 lb; and Extra Large (sometimes called "Whales"), over 25 lb.

Eastern Maine—Subarea XXII B: All the fish examined were taken from the Grand Manan Banks area in depths ranging from 30 to 70 fathoms and were examined at sea during Cruise 105 of the *Albatross III*. Of 390 fish examined 26 (8.9%) were infested.

Central Maine—Subarea XXII C: The only cod readily available for sampling in this north central section of the Gulf were landed in Manset, Maine, by a small group of draggers operating in the nearby Blue Hill Bay region. Twenty-four cod were available; of these 7 (29.2%) were infested and two had bilaterally attached parasites.

Western Maine—Subarea XXII D: The cod sampled from this region were caught near shore along that segment of the 50-fathom isobath which extends 20 miles southward from Cape Elizabeth, Maine. A total of 413 cod were examined; of these 36 (8.7%) were infested.

Small cod were not represented. This can be attributed to gear selectivity: all of the cod examined were landed by gill netters operating from Portland, Maine. These fishermen utilize a large mesh which is highly selective for bigger fish.

Inner Grounds—Subarea XXII F: This central area of the Gulf showed an infestation rate of 7.6%, based on 25 infestations found on examination of 331 cod.

There were very few small fish. The reason for this is again gear selectivity. The most characteristic feature of this section of the Gulf is its rocky shoaling bottom, which makes dragging hazardous at best. Cod, however, are found here in large numbers. The only efficient gear for use in these waters is hook and line; the absence of small fish in the catch is explained by the use of the large hooks, baited to attract the larger, more profitable, fish.

Eastern Massachusetts—Subarea XXII E: The cod examined from this area were landed by two groups of vessels: sport fishing boats and small commercial draggers, both operating in relatively shallow inshore waters, to 30 fathoms. Of 685 cod examined 51, or 7.5%, were infested. The landings of the commercial catch were examined at the port of Boston while those of the sport fishing boats were sampled at various small ports along the Massachusetts coast, including Plymouth, Scituate, Cohasset, Hull, Rockport and Gloucester.

Sampling in this area was rather evenly distributed through the different size categories. Two additional non-size categories were added: 1) heads, from those fish of about medium size which had been beheaded, and 2) mixed, cod of all sizes with length measurements unobtainable as a result of the rapid processing at the fish plants in which these samples were taken.

West Side of the South Channel—Subarea XXII G: The Boston medium trawler fleet often fishes heavily in this nearby area during the summer months. As a result, it was possible to examine 1122 cod. Of these, only 9 or 0.8% were infested. The distribution of infestation was about the same through all size categories.

East Side of the South Channel—Subarea XXII H: The Boston medium trawler fleet which fishes this area, located approximately 100 nautical miles east of Provincetown, remains away from port from 5 to 7 days. Such an extended period at sea coupled with the warm weather and melting ice in the fish hold during summer increases the danger of bacterial decomposition. For this reason the gills of all fish exceeding scrod size (2½ lb) are removed. In order to secure samples of intact cod from this offshore area it was necessary to make a trip aboard a commercial vessel. Examination of 193 cod revealed only two *Lernaeocera* (1.0%).

Northern Edge and Northeast Peak of Georges Bank—Subarea XXII J: This section of Georges Bank is fished intensively by the Boston large trawler fleet. Although the catch of these vessels comprises the bulk of New England cod landings it was rather difficult to secure samples. All the fish landed from vessels which remain at sea for upwards of 10 days during the summer months must by law have the gills removed. A limited number of cod with gills intact were secured by placing large canvas sample bas-

kets (200-lb capacity) aboard a few of the vessels. These were filled by the fishermen and examined at dockside when the vessel returned to port. However, the greatest number of cod were observed during a 10-day trip aboard the trawler *Wisconsin* and during Cruise 104 of the *Albatross III*. A total of 767 cod were examined and of these 14 (1.8%) were infested.

Rhode Island Shore—Subarea XXII S: This area, lying off Point Judith, was the southernmost sampled. A total of 212 cod landed by vessels of the local industrial fish fleet were examined. None was found with *Lernaeocera*.

Western Browns Bank—Subarea XXI P: The observations in this area were made during Cruise 105 of the *Albatross III*. There was only one infested cod found during examinations of 82 individuals (1.2%). All of the fish examined were taken in the shoal area (30–65 fathoms).

Western Nova Scotia—Subarea XXI Q: This sample was also secured on Cruise 105 of the *Albatross III*. Eight cod were examined and one of these was infested with two *Lernaeocera*, bilaterally attached. The observations were made on cod taken from some 6 miles south of the Lurcher Shoal Lightship in depths of 30 to 45 fathoms.

Northern Bay of Fundy—Subarea XXI S: The only reasonably accessible places for sampling in this region were the islands of Campobello and Grand Manan, located at the mouth of the Bay of Fundy. Here the daily catches of many family-owned small hook and line vessels are landed.

A total of 292 cod landed at the ports of White Head and Seal Cove, Grand Manan and Wilsons Beach, Campobello were examined. Of these, 95 or 32.5% were found to be infested with one or more *Lernaeocera*.

INFESTATION SELECTIVITY

The percentage of infestation by size for all samples is shown in Table 1. A χ^2 value of 2.12 (2 d.f.) demonstrated that there were no significant differences in infestation rates among the small, medium and large fish. A comparison of the extra large category was not made because of the small sample in this size range.

TABLE 1. *Percentage of infestation by size category*

Size category	No. of fish	No. of infestations	% infested
Small	1,381	83	6.0
Medium	2,121	114	5.4
Large	487	27	5.5
Extra Large	57	1	1.7
Heads	156	22	14.1
Mixed	293	20	6.8
No measurement	24	0	—
Total	4,519	267	5.9

CONDITION OF INFESTED FISH

Previous investigations on the effect of *L. branchialis* on the definitive host have been carried out in European waters (Schuurmans-Stekhoven 1936; Mann 1952; Capart 1948; Sproston 1942; and Kabata 1958). All reach the general conclusion that *Lernaeocera* is harmful to the definitive host, but fail to agree as to the extent of damage. However, their work involved several gadoid species not found in North American waters.

In the present study the length–weight regressions for infested and non-infested fish are almost identical:

Non-infested cod, $\log \hat{y} = -4.381 + 2.829 \log x$

Infested cod, $\log \hat{y} = -4.543 + 2.915 \log x$

Where x = length in mm and y = weight of eviscerated fish in lb.

Neither the intercepts ($t = 1.3500$; d.f. = 89) nor the slopes ($t = 1.2818$; d.f. = 89) show significant differences. Superficially the infested cod appeared healthy; their flesh was firm and their skin coloration similar to that of non-infested fish. However, in the absence of age data, there is no evidence that their growth rate was normal.

There was no significant difference in infestation rates between various size categories of fish. It can be concluded, therefore, that the parasite does not select its definitive host by size or cause a differential death rate.

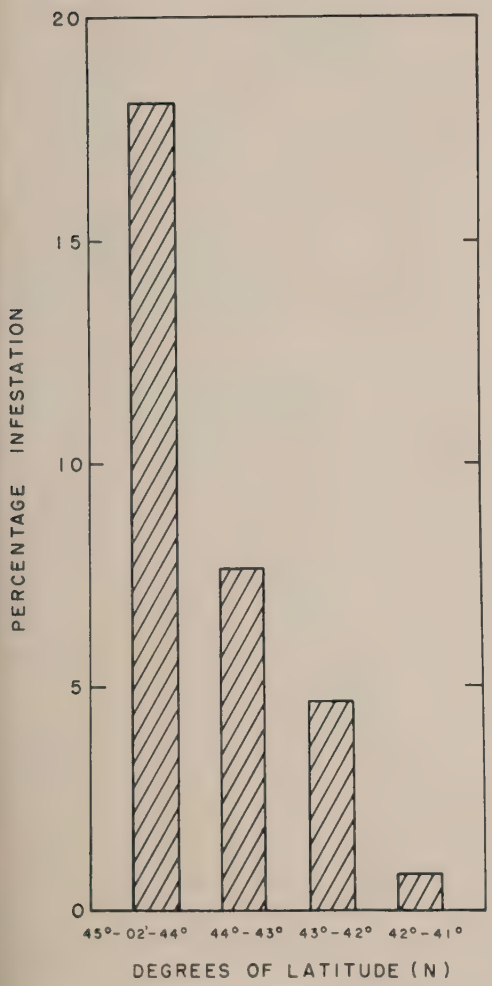

FIG. 2. Percentage infestation by latitude.

DISTRIBUTION OF INFESTATION

A differential occurrence of *Lernaeocera* on cod is present in New England waters. It is evident that the infestation rates assume a pattern of decreasing intensity from north to south in the region of investigation (Fig. 2). This fact, when considered with the Atlantic occurrence of the copepod, indicates that it is an organism of the boreo-arctic regions.

The vicinity of Cape Cod has long been recognized as the zone of transition between the boreal and temperate fauna. That this area would represent the southern limit in abundance of boreal species such as *Lernaeocera* or the lumpfish (*Cyclopterus lumpus*) is therefore not surprising. However, the cod extends its general range both south and west of Cape Cod in sufficient numbers during the winter months to support a fishery in the vicinity of Cape May, New Jersey (Wise 1958). In the present study this southern group of cod as represented by the XII S sample was found free of infestation while those to the north presented an increasing gradient of infestation northward.

Fish taken within 20 miles of the shore (13 to 40 fathoms) had an 8.3% infestation compared with 3.0% for those taken more than 20 miles from the coast. A similar gradient is characteristic of infestation of gadids by *Lernaeocera* in other areas. Templeman (1953) reported a similar situation in Newfoundland waters and Sproston and Hartley (1941) and Kabata (1957) in the coastal waters of Great Britain. Sproston (1942) concluded that infested fish do not migrate with the main stock, thereby increasing the inshore and estuarine infestation rates.

The inshore-offshore infestation pattern parallels the distribution of the intermediate host, the lumpfish, which according to Bigelow and Schroeder (1953) are restricted to a depth of a few fathoms in the Gulf of Maine. It would seem, therefore, that infestation will only occur in the shallow inshore waters of the Gulf when both the lumpfish and cod coincide there. The wide lateral distribution of the adult *Lernaeocera* may be explained by the movements of the cod, which are far less restricted (Bigelow and Schroeder 1953) than those of the lumpfish.

Sproston and Hartley (1941) estimated the minimum length of the gadid life cycle phase of *Lernaeocera* to be 8 weeks. They also found that no definite breeding period could be assigned because four or five consecutive generations were produced year-round, with a great degree of overlap. The percentages of infestation in the present study, although established only during the warmer months of the year, become more reliable as indicators of actual conditions

when supported by the results of Sproston and Hartley.

Bigelow (1927) described the dominant non-tidal circulation pattern in the Gulf of Maine as a general anticlockwise eddy. This, when considered with both the drift bottle data of Fish and Johnson (1937) and the drift pattern of the boreal pteropod *Limacina retroversa* (Redfield 1939), suggests that *Lernaeocera* will tend to be localized in the Gulf. The distance traversed by any individual larva would be negligible because of its limited (about 24 hr) planktonic existence. It is most likely that significant dispersal is accomplished during the time the larvae are attached to a host. If Bigelow and Schroeder (1953) are correct concerning the distribution of the lumpfish it becomes evident that all newly fertilized female copepods originate in shallow inshore waters. Because of their limited duration of planktonic life, they must encounter a definitive host in this area. Consequently, horizontal dispersal would be determined largely by the presence of cod during this critical time of *Lernaeocera* development.

The tagging experiments of Schroeder (1930) and Wise (1958) indicate a discrete self-contained population of cod in the area south of Nantucket Shoals. The results of the present investigation lend support to this conclusion. No infestation was found in the Middle Atlantic–Nantucket Shoals group sampled at Point Judith, Rhode Island, during the autumn migration. The light infestation found on Georges Bank and in the South Channel area indicate little mixing beween this group and those to the north and south. Moderate infestation in the central Gulf and heavy infestation of the northern coastal region suggests that mixing between these groups occurs regularly.

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SEROLOGICAL TECHNIQUES IN FISHERY RESEARCH

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Very early in the twentieth century, two events occurred that have only recently begun to affect the course of fishery research. Karl Landsteiner (1901) observed that the red blood cells of one human could be agglutinated or clumped by serum from another, and he proposed the ABO blood group system familiar to us today. In that same year G. H. F. Nutall (1901) published the first of a series of papers demonstrating that an antiserum reactive with serum proteins of one species of animal would also react with related species, thus instituting the science of systematic serology. Since these basic observations were made, and particularly since World War II, knowledge of human blood groups has advanced, so that now many human blood group systems have been proposed in addition to Landsteiner's ABO system (summarized by Mourant 1954, Race and Sanger 1954). We can now characterize an individual human being serologically with remarkable precision, and we can describe each human population serologically with similar precision.

Immunogenetic information has also been accumulated for cattle and chickens. Cattle blood group systems surpassing human systems in complexity have been developed as a tool in herd lineage studies. Work in the last decade has suggested that blood types of chickens

may be associated with characteristics such as egg production. Sheep, buffalo, pigs, whales, pigeons and doves have also been examined serologically, but until recently many of the other animal groups had been virtually ignored. This was particularly true for the fishes, and is still generally true with but a few exceptions.

This paper is concerned with those exceptions—with the progress and status of research in fish serology. It has several objectives: (1) to point out the scope of serological methods available to fishery research; (2) to demonstrate that fish serology is approaching the stage of quantitative studies; (3) to suggest the potential utility of serological or blood grouping studies to every investigation of marine animals; and (4) to indicate how serology has provided information of value to our own investigations of sea herring and certain other fish species of the western North Atlantic.

Systematic serology is based on three assumptions, which are receiving increasing support with the passing years: (1) that animals have evolved biochemically as well as morphologically, so that biochemical characteristics can provide as valid criteria for fish systematic studies as morphological and morphometric characteristics; (2) that many of these biochemical characteristics are genetically determined, and are not affected by environmental influences; and (3) that subpopulations within a species may be distinguishable by the existence of constant quantitative differences in the frequency of occurrence of particular genes when any two groups are compared.

Immunogenetic studies of fishes have a remarkably brief history, mostly confined to the past 10 years. At present I know of only eight groups in the world with major continuous research activity in this field: the U. S. Bureau of Commercial Fisheries Biological Laboratory at La Jolla, California, concerned with sardines (Sprague and Vrooman, personal communication); the U. S. Bureau of Commercial Fisheries Biological Laboratory at Seattle, Washington, working with salmon racial separations based on blood types (Ridgway, Cushing and Durall 1958, Ridgway and Klontz 1960); the Nankai Regional Fisheries Research Laboratory in Japan concerned with tuna blood groups (Suzuki, Shimizu and Morio 1958); the Fisheries Research Institute at Ijmuiden, Holland, concerned with North Sea fish (de-Ligny, personal communication); Dr. Cushing at the University of California, Santa Barbara, one of the pioneers in fish serology, who has been interested in a number of species including tuna (Cushing 1952a, 1952b, 1956, Cushing and Sprague 1952, 1953); the U. S. Bureau of Commercial Fisheries Biological Laboratory in Honolulu, Hawaii, working with tuna and bait fish (Sprague, personal communication); Dr. O'Rourke of University College, Cork, Ireland, who is

interested in several species of marine fish (O'Rourke 1959); and our laboratory, the U. S. Bureau of Commercial Fisheries Biological Laboratory at Boothbay Harbor, Maine, concerned with several commercial species from the western North Atlantic, particularly herring (Sindermann and Mairs 1959).

Most of the emphasis so far has been placed on development of techniques, so there is still little quantitative information available, but everyone working in this field is firmly convinced of and very enthusiastic about its potential value to fishery research, once exploratory work has been accomplished. In the published literature, blood group systems have been described for tuna and Atlantic herring. Quantitative studies have described subpopulations of Pacific salmon and Atlantic herring, and indications of antigenic differences that may be of potential value have been found in over 20 species of fish.

PROBLEMS AMENABLE TO SEROLOGICAL APPROACHES

It might be instructive to look at some of the specific fishery problems that we in the immunogenetics group at Boothbay Harbor have considered. These are illustrative of the kinds of problems that may be amenable to serological investigation, although there are undoubtedly many applications that have not even been visualized.

(1) Immature herring (*Clupea harengus*) are caught in the Gulf of Maine and canned as sardines. The origin of these small fish is unknown. We know there are major spawning areas on the Nova Scotia coast and on Georges Bank off Cape Cod, but we do not know if either or both contribute to the coastal sardine-herring stocks.

(2) Atlantic redfish (*Sebastes marinus*), caught on the major fishing banks of the western North Atlantic, are of great commercial importance. We do not know if these are fringes of a large pelagic oceanic population, or if they represent discrete subpopulations. Furthermore there are pronounced morphological differences suggestive of possible subspecies.

(3) In recent years there have been increasing reports of large sharks in inshore North Atlantic waters. More information is needed about subpopulations and migrations of many shark species, from dogfish on up to those that cause closing of beaches.

(4) Along the Atlantic coast are five major species of clupeoid fishes, and several minor species. The natural relationships of these species—indeed of many comparable groups of fish—are subjects of conjecture and argument. Further fundamental studies are needed.

These are some of the problems to which we have applied serological

approaches, and for which we have in some instances partial answers. I propose to concentrate on our own work at Boothbay Harbor, but you must recognize that comparable problems are being examined serologically in the other laboratories already mentioned with equal or possibly greater success.

1. *Herring Subpopulations*

Insights into the nature of herring subpopulations have been gained with a blood group system described earlier as the C system (Sindermann and Mairs 1959). Cells from individual fish were tested against antisera prepared by injecting herring erythrocytes into rabbits. In appropriate dilutions of such antisera cells of some herring clumped or agglutinated very weakly if at all, while cells from other herring reacted and agglutinated strongly, even in higher dilutions of the antiserum. This suggested that some individuals possessed a factor (an antigen) on their red cells that other individuals lacked. We labelled this factor or antigen "Antigen C" and characterized fish as C-positive if they possessed the antigen, or C-negative if they lacked it. The antiserum was further refined as a reagent for detecting antigen C on herring blood cells by antibody absorption. Absorption is the critical technique in all cell antigen research, and is the key on which much of the future of this work depends. It is actually a fractionation method to get specific test reagents (Fig. 1).

With such a reagent we tested blood samples taken along the Maine coast for frequencies of antigen C. Tests of over 2000 individuals clearly demonstrated population heterogeneity, and disclosed the existence of 2 subgroups, eastern and western, probably drawn from different spawning populations (Fig. 2). The next step was to sample known major spawning populations (Georges Bank and Nova Scotia) for the frequency of this antigen, in an attempt to relate the immature sardine-size fish to spawning groups. This was done, and the tests indicated that the major known spawning groups could contribute to eastern sardine herring stocks (Fig. 2), but that we must look elsewhere for the source of at least part of the western stocks, since the frequencies of antigen C were lower in western stocks than in either major spawning group. We have since looked in the Gulf of Saint Lawrence and on the Rhode Island and New Jersey coasts for the spawning group with relatively low antigen frequency that we knew must exist. Recently we tested a small sample of inshore spawners from the southern Gulf of Maine that had such a low frequency. Although much more extensive sampling must be done in this area, this suggested an inshore source of western sardine herring stocks.

The possibility still existed that the eastern stocks could be drawn

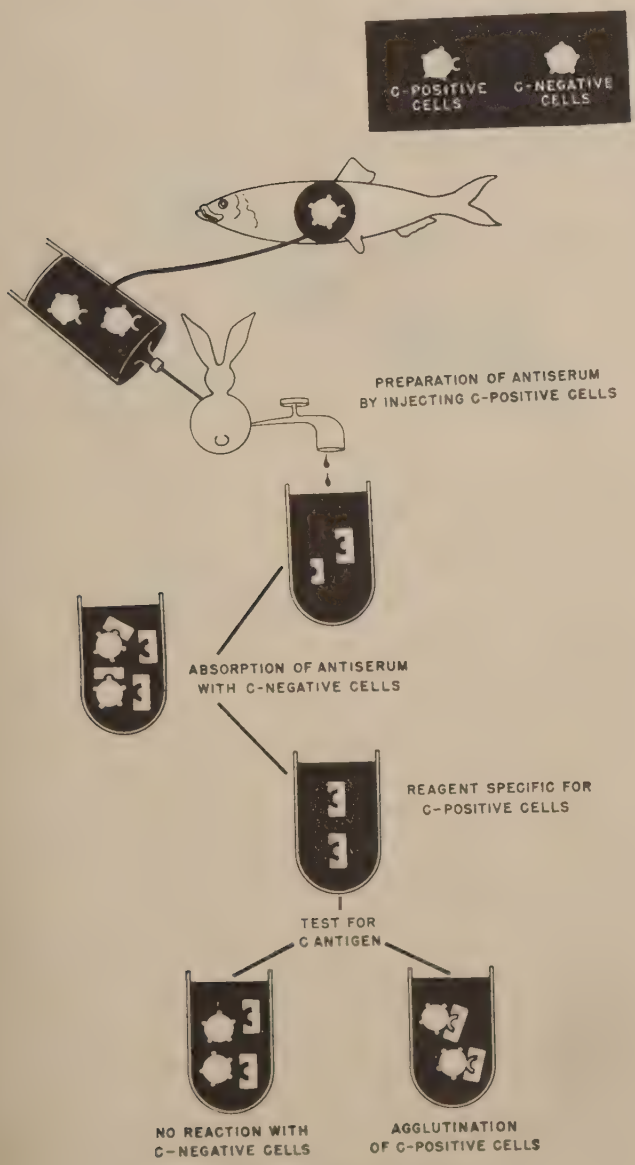

Figure 1. Absorption of herring C reagent.

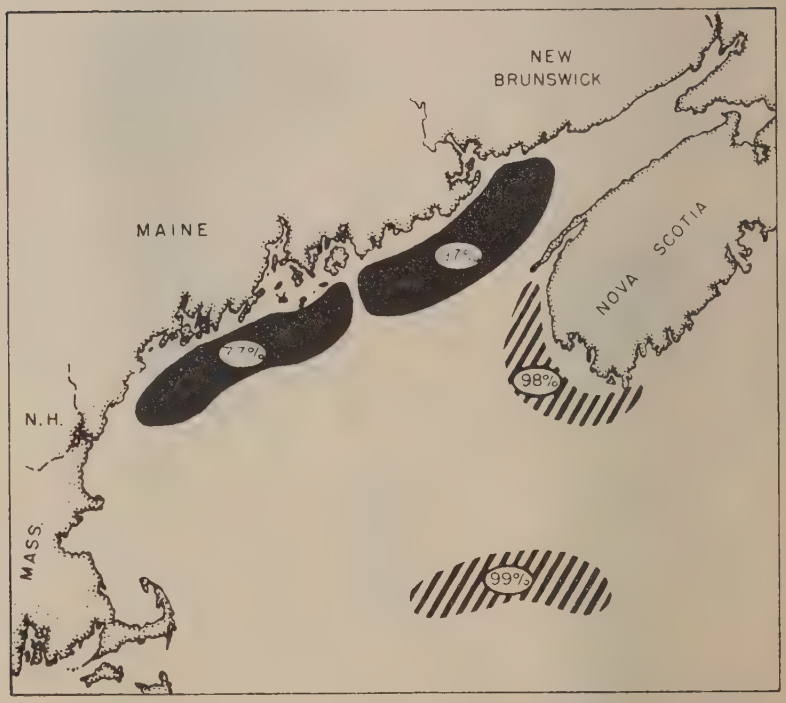

Figure 2. Antigen C frequencies in immature herring (black areas) and in major known spawning populations (diagonal bars).

from either or both of the major spawning populations—Georges Bank or Nova Scotia—and we needed another system that would differentiate between the two, since the frequencies of antigen C would not. By injecting rabbits with herring cells that were negative with the C reagent, antisera were produced that would differentiate, after absorption, another antigen with reactions independent of the C system. We have done preliminary tests of both major spawning populations for the frequency of this new antigen, called antigen "D," and have found it significantly higher in the Georges Bank population. We have recently begun sampling and testing the eastern sardine stocks for the frequency of the D antigen. Results of the first tests relate them definitely to Nova Scotia spawners. More data are needed, but we feel that we are approaching the solution to a problem that has remained unsolved for over half a century—the origin of east coast sardine herring stocks.

Tests with the herring blood group antigens have indicated that we should consider our sardine herring stocks as two separate entities in any future management plans and have suggested the spawning populations that we must scrutinize to understand reasons for the characteristic drastic fluctuations in abundance of immature herring from year to year. With these and other blood factors yet to be discovered, an interlocking characterization of each individual fish and each subpopulation can be achieved eventually, so that just as individual humans can now be completely characterized or typed, and human races and subgroups identified by frequencies of each blood type, so also individual herring may be described eventually as C^+, D^-, E_2, F_o etc., and herring subpopulations described by frequencies of each factor. At that point we will be able to give an excellent approximation of the discreteness or intermixing of subpopulations and their subsequent movements, on the basis of red cell reactions alone.

2. *Dogfish and Redfish Blood Group Systems*

We have had greatest serological commitment with herring, but have recently completed some work with sharks that has proved even more exciting and definitive. This grew out of interest in the increasing reports of larger shark species along the coast of the northeastern states—in 1960 particularly, when beaches were closed repeatedly by shark scares. We felt that immunogenetic methods could be applied to studies of shark subpopulations and migrations as well as to bony fish. We examined the east coast spiny dogfish, *Squalus acanthias*, to see if antigen differences could be detected that might be used in migration work, as a pilot study for the larger shark species (Sindermann and Mairs, in press). An isoagglutination system which we have labelled the S system was found to exist in this species, with two erythrocyte antigens, S_1 and S_2. Individuals may possess both, either or neither antigen, being of types S_1S_2, S_1, S_2, or S_o respectively. S_1 antigen can be detected by isoagglutinins in sera of dogfish which lack the antigen while either S_1 or S_2 can be detected with rabbit antisera absorbed with S_2 and S_1 cells respectively. A flow diagram illustrating this work is shown in Fig. 3. We have had the added advantage of being able to type unborn young from gravid females and to compare these with the parent female. This has provided genetic information that is so difficult to acquire for most marine fish. The dogfish S system is convincing evidence to us that there is order in what we work with, and now awaits quantitative studies of antigen frequencies in dogfish populations.

Blood groups in another commercial marine species, the Atlantic redfish, *Sebastes marinus*, have been examined (Sindermann in press). This species is widely distributed and abundant in the North Atlantic,

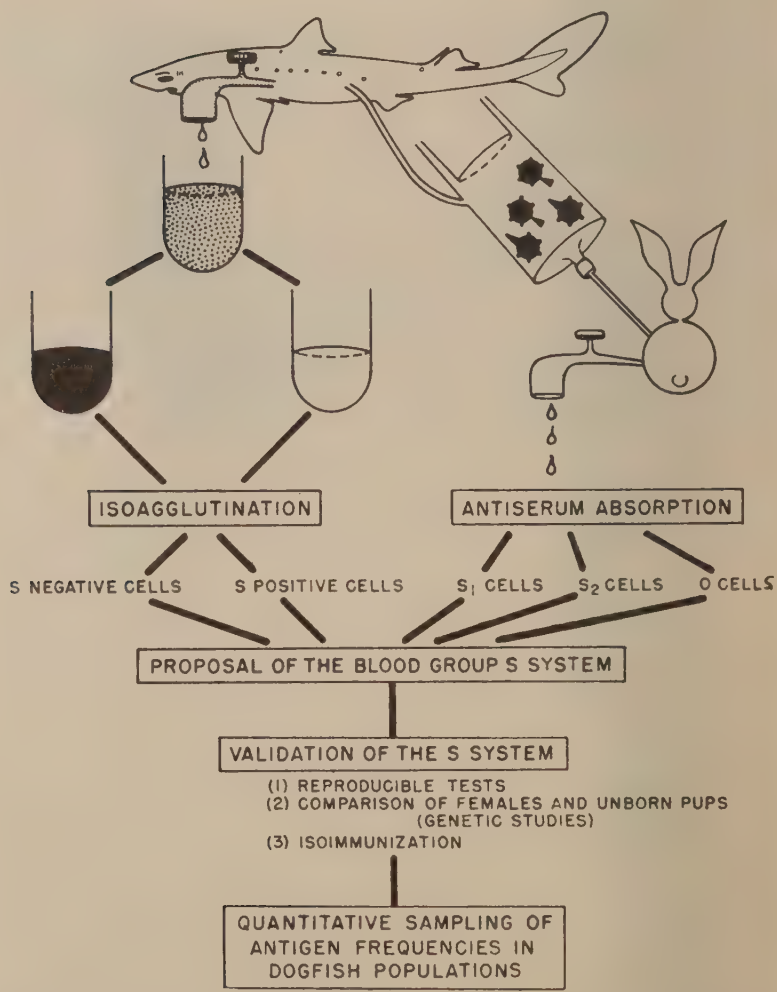

Figure 3. Flow diagram of dogfish studies. Isoagglutinins in dogfish sera and antibodies remaining in absorbed rabbit antisera are used simultaneously to determine the presence or absence of S antigens.

and is almost impossible to tag. A one-week symposium on its taxonomy in Copenhagen (1959) failed to reach agreement about intraspecies groups using traditional methods. We have proposed a first blood group system for redfish, the "A" system, comparable to the human ABO and the dogfish S systems in that it is composed of two

antigens, A_1 and A_2. Individuals may possess both, either, or neither antigen. Specific reagents, produced by antiserum absorption, will detect either antigen. So far quantitative data are limited to one geographic area (Eastport, Maine) where A_1 occurs in over 75% of the fish. If comparable sampling of each major fishing ground is done, we should be able to determine discreteness of geographic groups.

3. *Serological Relationships of Five Species of Atlantic Clupeoid Fishes*

Subpopulations within a species have been considered thus far in this paper, but serology can have a major role in solving taxonomic problems above the level of species as well. We have examined the five dominant clupeoid species of the western North Atlantic: herring (*Clupea harengus*), alewife (*Alosa pseudoharengus*), blueback (*Alosa aestivalis*), shad (*Alosa sapidissima*), and menhaden (*Brevoortia tyrannus*). Their serological relationships—the relative serological distances that presently separate species—have been determined with a combination of several techniques, using both cells and serum. Methods used were precipitin tests visualized photoelectrically and by agar diffusion, erythrocyte agglutination with absorbed antisera, and electrophoresis. With this composite approach we have achieved a model representing the relative serological distances separating the five clupeoids (Fig. 4). Alewives and bluebacks were found to be serologically very similar, while herring were serologically remote from the others. Shad were closer to the alewife-blueback complex than were menhaden. This composite method provides another criterion that can be used in taxonomic studies, along with morphological characters such as gill rakers, teeth, scale counts, fin position, etc. It actually does much more than this. It supplies a method for separating closely related species, many of which may be difficult to separate morphologically, especially in young stages. Also, it provides a tool for recognition of species hybrids, since hybrid values fall between those of the two parent species. Most importantly, from our point of view, this work gives us background for comparable studies of subpopulations within a species. These would complement studies using blood group systems, and would provide greater serological depth. Actually, there is a whole spectrum of methods that could and should be explored in this composite approach to systematic problems, including such things as serological comparison of egg proteins or sperm antigens.

THE SEROLOGICAL FUTURE

It seems clear that serology, especially that part of it concerned with blood group antigens, will soon become a standard method in

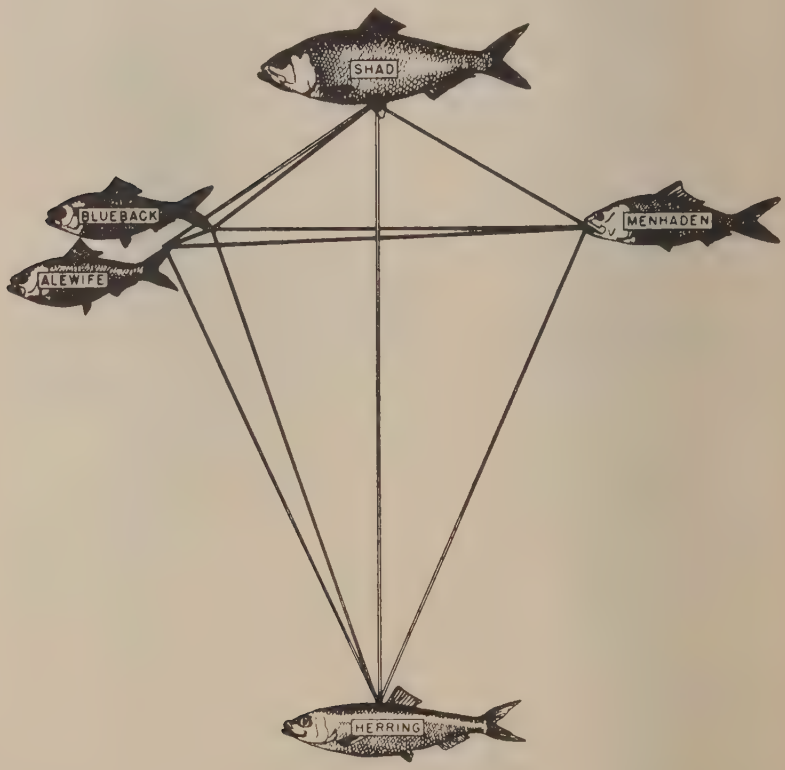

Figure 4. Serological relationships of five clupeoid species.

fishery biology. Systematic problems in any group of animals, at any taxonomic level, should be susceptible to investigation by one or several of the many serological approaches available. Population, racial, or subspecies problems are amenable to these techniques, and wherever you look in fishery research, whether in fresh-water or in the sea, there are problems, some of them of long standing, for which serological methods may provide definitive answers.

Comparable studies of marine invertebrates should be as rewarding as studies of fish. Antigenic differences have been detected among geographic races of Japanese oysters (Numachi, 1959) and it is possible that information about subpopulations and migrations of other species such as crabs, lobsters or shrimp could be derived from serological investigations.

With the increasing attention to and exploration of serological tools

in several laboratories in the United States and other countries, the pace of research has accelerated. Once our period of groping and pilot studies is over, we should have another criterion, reasonably unaffected by environment, available for the study of subpopulations and migrations of fish—a criterion which should take its place beside more traditional methods, and may in fact prove ultimately of greater utility than such methods. The future seems limited only by the extent of our commitment.

SUMMARY

During the past decade there has been increasing interest in the use of serology for systematic studies of fishes. Of the varied techniques available to serology, investigation of red blood cell antigens, and subsequent description of blood group systems to contain them, offer greatest promise to the understanding of intraspecies groups. Quantitative study and comparison of antigen frequencies in fish from different geographic areas may provide information about the degree of intermixing and movement of subpopulations within a species. It is becoming apparent that discrete individual differences in red cell antigens characterize teleosts as well as higher vertebrates, and that geographic variations in antigen frequencies may be expected. Tuna, salmon, sardines and herring have been examined serologically, and quantitative information identifying geographic groups has been published. Blood group systems have been proposed for tuna, spiny dogfish, herring and redfish, and individual differences in erythrocyte antigens noted in many other species of fishes.

The practical aspects of serological work are exciting indeed. Since information derived is genetic, it will be possible to assess the discreteness of stocks or groups of fish for management purposes. Herring of the Gulf of Maine have been characterized in this way. Furthermore, it is possible to relate stocks of immature fish to specific spawning aggregations by these methods. This work is also in progress with Atlantic herring. As more marine laboratories begin blood group research, and as methods are refined, serology should become a standard method in fishery research, providing information about stocks and movements of commercial species, as well as supplying a tool for basic studies of subpopulations and the genetics of marine fishes.

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DISCUSSION

DISCUSSION LEADER CHAPMAN: This has been a fascinating paper. The new technique of serology as applied to fisheries racial problems is becoming one of the most useful tools that has been developed in our work in a long while. We have on our coast the problem of dealing with the yellowfin tuna, stretching over an area of about 4,000 miles from north to south, and it is an absolute necessity to get them separated into homogeneous populations for conservation regulation. None of the other normal techniques used in this work has had any effect, and serology is beginning to provide us with, we hope, a satisfactory tool to deal with that problem.

MR. SILLIMAN [Fish and Wildlife Service, Washington, D. C.]: You stated that you were using blood serum for sardine differentiation. Dr. Ridgway in Seattle, working on salmon, is also using this. He has recently been experimenting with plant proteins and I would like to ask your opinion of these serums.

DR. SINDERMANN: Plant extracts have been used and are being used with success by a number of people working in fish serology. We have tried plant extracts and started early with them. We found that the extracts were distinguishing the same C system that was distinguished by our rabbit anti-serum. I feel that there is a broad avenue of research in plant extract work, and I think that it will be pursued more vigorously. We have had initial success with rabbit anti-sera of fairly high specificity, so we have clung to this.

I might say though that we have recently tried using elasmobranch fishes as sources of anti-serum, and we find that the dogfish is an almost ideal experimental animal. It yields large quantities of blood and produces quite specific anti-serum. We plan to extend our studies, using both dogfish and skates during the coming season.

We have been using with the C system the same anti-serum that we developed three years ago and we still have good supplies of it. When you do absorptions selectively for some of the antibodies, you use up anti-serum fast. Normally the rabbit produces sufficient quantities for our work.

It might be true that if you were going to do a continuing population study as it should be done, you might run into difficulty. We feel safe, however, since we can turn to these plant extracts if we ever run short of our original C reagent.

67. **Sporozoan Parasites of Sea Herring.** CARL J. SINDERMANN, U. S. Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine.

As part of a continuing investigation of marine fish diseases, sporozoan parasites of sea herring, *Clupea harengus*, have been studied. Five species have been recognized: *Kudoa clupeidae* and *Ceratomyxa acadiensis* (Myxosporidia); *Eimeria clupearum* and *Eimeria sardinae* (Coccidia); and *Plistophora sp.* (Microsporidia). *Kudoa clupeidae* has been reported previously (Sindermann, 1957, J. Parasit. **43**: 42–43) as an intramuscular parasite with a discontinuous distribution in immature herring of the western North Atlantic. *Cerotomyxa acadiensis* has been found in the gall bladders of several marine fish species from Canadian Atlantic waters, and is reported here as an occasional parasite of immature and mature sea herring. Two species of *Eimeria* occur in herring, although neither have been reported previously from the western Atlantic. *E. sardinae* occurs only in the testis, occasionally in great numbers in individual fish. This parasite has been reported to cause castration of European sardines (Santos-Pinto, 1957, Univ. Lisboa, Revista **5**: 5–9). *E. clupearum* is a common parasite of the liver, especially of adult herring. *Plistophora sp.*, a microsporidian, was found in intramuscular cysts adjacent to the body cavity of very young herring, but has not been seen in fish over 9 months old.

Samples of herring of all sizes, distributed geographically from New Jersey to the Gulf of Saint Lawrence, have been examined yearly since 1955 for sporozoan and other parasites. Incidences of the Sporozoa mentioned in this paper have been less than 25 percent except for *Kudoa clupeidae*, which may occur in up to 80 percent of 1-year-old herring from certain coastal areas. Marked year to year variations have been noted only for *Kudoa* in which a continued downward trend in incidences has occurred, but it may well be that longer-term studies will disclose periodic characteristics of this and other parasites of marine fishes.

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EXTRAIT
Rapp. et Proc.-Verb. Vol. 150, 1961
Cons. Internat. Explor. de la Mer

B. 4

Serological Studies of Redfish[1])

By
CARL J. SINDERMANN
U. S. Bureau of Commercial Fisheries, Boothbay Harbor, Maine

Abstract

During the past decade there has been increasing interest in the use of serology for systematic studies of fish. Of the varied techniques available to serology, investigation of erythrocyte antigens, and subsequent description of blood group systems containing them, offer greatest promise to the understanding of infraspecies groups. Quantitative study of antigen frequencies in fish from different geographic areas may provide information about the degree of intermixing and movement of populations within a species.

As the first phase in such a programme for redfish, *Sebastes marinus*, from the North Atlantic, individual variations in cellular antigens have been examined. The existence of two closely related antigens, tentatively labelled "A_1" and "A_2", has been demonstrated with specific reagents created by absorptions of rabbit antisera. Each reagent would agglutinate cells of only one antigenic type, so it was possible to identify fish as possessing A_1 or A_2 antigen. Although much more extensive sampling is needed, it has been found that individuals with the A_2 erythrocyte antigen make up less than 10 % of the Eastport (Maine) redfish population. Since antigen frequencies may vary from one population to another, quantitative studies of each major fishing area should provide further information about discreteness of the groups involved.

In addition to quantitative studies of A antigen frequencies, search should be made for other antigens and systems in redfish, to enable more precise characterization of each population. Serology can then constitute an important criterion, along with traditional morphometric and meristic studies, for understanding the infraspecies structure of redfish.

1) The complete paper in Fish. Bull. U.S. Fish & Wildl. Serv., *61*.

EXTRAIT

Rapp. et Proc.-Verb Vol. 150, 1961
Cons. Internat. Explor. de la Mer

B. 3

Parasitological Tags for Redfish of the Western North Atlantic

By
CARL J. SINDERMANN
U. S. Bureau of Commercial Fisheries, Boothbay Harbor, Maine

Introduction

Parasites and diseases of animals may vary in abundance geographically, so that individuals sampled in one area may be recognized by certain frequencies of particular parasites, or even by parasites that are not found in another area. If we can characterize marine fish in this way, by assessing parasite frequencies on each fishing ground, or in spawning aggregations, it should be possible to determine the nature and extent of movements, if any. This method has already been applied with some success to sea herring of the western North Atlantic, which have been found to participate in only local movements (Sindermann, 1957a; 1957b). Some information has also been gained about redfish (*Sebastes marinus*) stocks of the western North Atlantic by studying the distribution of a single parasite, the copepod *Sphyrion lumpi* (Herrington, 1939; Templeman, 1950; Knapp-Fisher, 1952; Perlmutter, 1953). Lüling (1951) noted that redfish from different grounds off Iceland varied widely in incidence of larval nematodes (Anisakinae). Since redfish from deep water are difficult to tag, a detailed study of parasites as "natural marks" may be a method of choice in population and migration studies.

Since the discontinuous distribution of *Sphyrion* in redfish of the western North Atlantic had already indicated lack of extensive movements of host fish, it seemed that by examination of the distribution of other redfish parasites, it might be possible to determine the precise amount of interchange, if any, among the major fishing grounds. Although much more intensive sampling over a long period is needed, results to date have been informative and are presented in this report.

Methods

Redfish samples of 100 fish each were obtained from otter trawlers unloading at Rockland, Maine, and Gloucester, Massachusetts. Figure 1 shows locations of major fishing grounds sampled. Only fish of commercial size were examined, so individuals below the minimum size for filleting (approximately 15 cm) were not included. Some selection for size was also imposed by the nature of the catches, since some were composed principally of smaller fish (as in Grand Banks samples) and others were composed principally of larger fish (especially Cape Cod Highlands and Gulf of Saint Lawrence samples). Although not determined in the present study, the age of the fish may affect its parasite burden. This is a factor that should be investigated in any future large-scale parasite sampling programme.

When possible, several samples taken during different months were obtained from each area. Fish were examined individually for the following parasites:–

(1) *Sphyrion lumpi* – an ectoparasitic copepod with its anterior end permanently embedded in the body of the host;
(2) *Chondracanthopsis nodosus* – an ectoparasitic copepod attached to the basal portions of the gills;
(3) *Ichthyosporidium hoferi* – a systemic fungus parasite which produces white nodules on and in the heart, spleen, and liver;
(4) Trypanorhyncha – larval cestodes encysted in the stomach wall and adjacent mesenteries; and
(5) Anisakinae – larval nematodes, encysted or migratory, in the viscera.

The parasite fauna of redfish is much larger than this, but the parasites listed were selected because they could be recognized readily, because they seemed to be relatively permanent, and because in preliminary work they were found to vary in abundance geographically. All parasites were preserved for subsequent identification, and incidence of each species was recorded for each major fishing area.

Results

Photographs of certain parasites considered in this study as "natural tags" are included in Figure 2. Average incidence in each major fishing area is summarized in Table 1, and data from each sample are included in Table 2.

The data illustrate the often dramatic differences in abundance of certain parasites on different fishing grounds. In some cases such as *Sphyrion,* Trypanorhyncha, and *Ichthyosporidium* the parasite was absent from samples taken in certain areas, but was abundant in other areas. There was no evidence that the

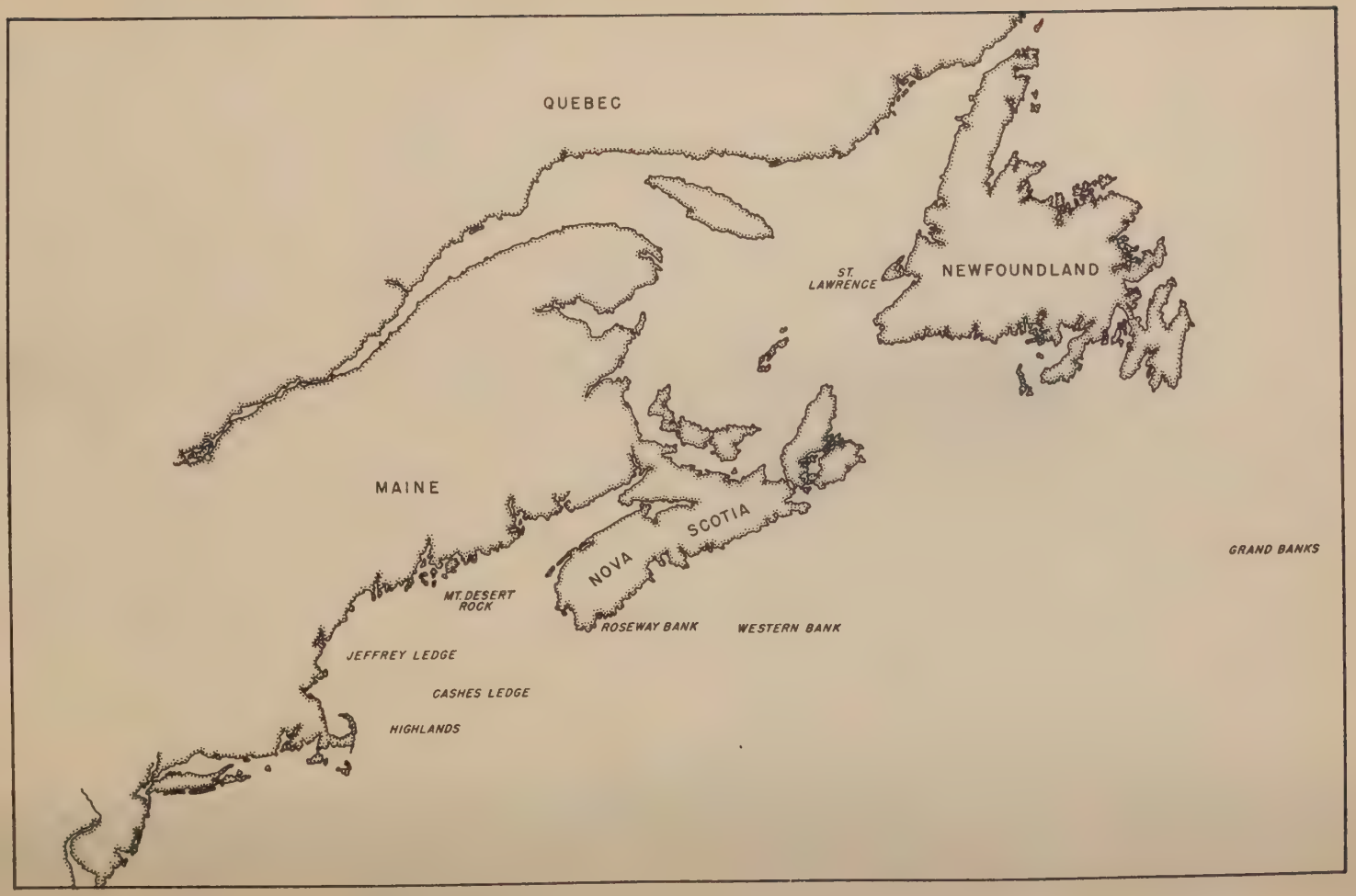

Figure 1. Locations of major fishing grounds sampled in the present study.

Table 1
Parasite incidences in redfish of the western North Atlantic

Fishing Ground	Parasite Incidences (%)				
	Sphyrion lumpi	*Chondracanthopsis nodosus*	*Ichthyosporidium hoferi*	Trypanorhyncha	Anisakinae
Grand Banks	0	14	1	0	7
Western Bank	0	46	5	25	10
Roseway Bank	0	25	0	22	69
Mount Desert Rock	24	23	0	50	56
Jeffrey Ledge	0	8	0	46	68
Cashes Ledge	14	13	0	26	31
Cape Cod Highlands	9	6	0	14	45
Gulf of Saint Lawrence	0	2	1	0	21

Table 2
Results of parasite examination of redfish

Fishing ground	Dated sample (1959)	Parasite Incidences (%)				
		Sphyrion lumpi	*Chondracanthopsis nodosus*	*Ichthyosporidium hoferi*	Trypanorhyncha	Anisakinae
Grand Banks	Jan.	0	15	1	0	8
	Mar.	0	12	0	0	6
Western Bank	Jan.	0	45	6	–	10
	Jan.	0	48	3	25	–
Roseway Bank	May	0	25	0	22	69
Mount Desert Rock	Jan.	25	21	0	50	56
	Jan.	22	26	0		–
Jeffrey Ledge	Jan.	0	8	0	46	68
Cashes Ledge	Mar.	14	13	0	26	31
Cape Cod Highlands	Mar.	9	6	0	14	45
Gulf of Saint Lawrence	July	0	1	1	0	21
	Aug.	0	–	0	0	–
	Aug.	0	4	0	0	–

abundance of one parasite was in any way influenced by another, although factors such as temperature, depth, presence of intermediate hosts, and proximity to shore may have had an effect. There was no definite evidence for seasonal variation in frequency of parasites, although more extensive sampling might modify this finding.

Sphyrion lumpi was found only on fish from the Gulf of Maine, with a peak abundance in the Mount Desert Rock samples. More detailed studies of the distribution of this copepod in the Gulf of Maine have been made previously (Herrington, 1939; Perlmutter, 1953; Kelly, 1957) and incidences reported here agree well with published data. Greater numbers of samples might disclose very low incidences of this and other parasites in certain areas listed as negative. This proved to be the case in extensive sampling for *Sphyrion* reported by Templeman (1950) and Knapp-Fisher (1952).

The gill copepod, *Chondracanthopsis nodosus*, reached a peak of abundance in samples from Western Bank, and decreased in the southern Gulf of Maine, while larval nematodes (Anisakinae) were least abundant on the offshore banks. Larval cestodes (Trypanorhyncha) were absent in Grand Banks and Gulf of Saint Lawrence samples, and were most abundant in the northern Gulf of Maine. *Ichthyosporidium hoferi*, the fungus parasite, was absent from Gulf of Maine samples, and was found only in fish from Western and Grand Banks and the Gulf of Saint Lawrence.

Discussion

It should be possible with data such as these to determine with some precision the maximum possible interchange of redfish between any two fishing grounds. This method considers parasites and parasite frequencies as characteristics of stocks in any particular area, and is based on the following assumptions:–

(1) that the parasite is relatively permanent – persisting for at least several years;

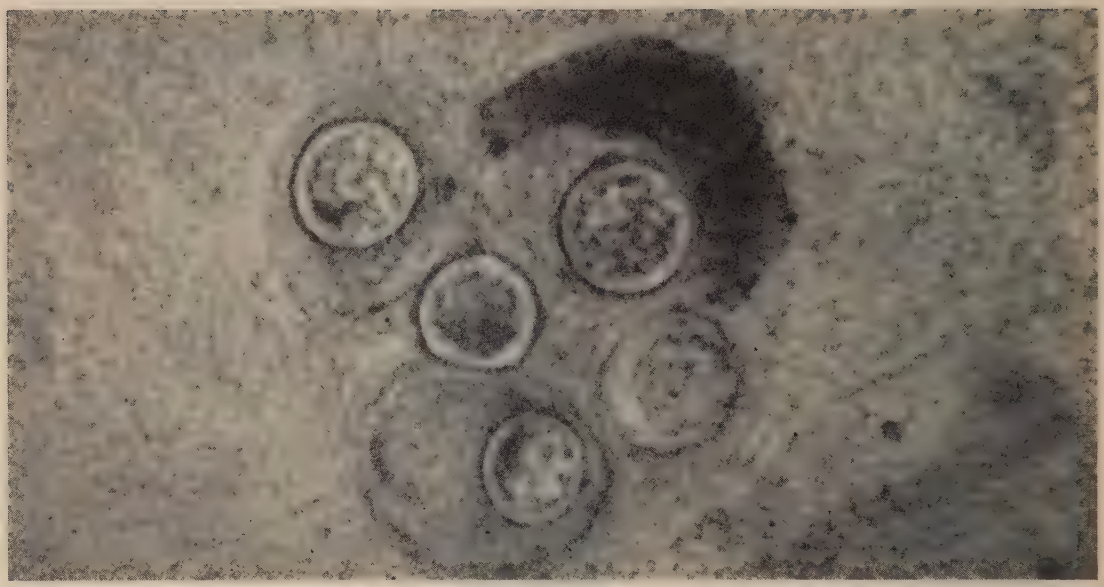

Figure 2. Parasites used as "natural tags" for redfish.
(a) Photomicrograph of spores of the fungus *Ichthyosporidium hoferi* in a redfish heart. Spores range in diameter from 30–60 microns, are characteristically multinucleate with a heavy spore wall, and are encapsulated by host connective tissue. The parasite produces white nodules on heart, liver and spleen.

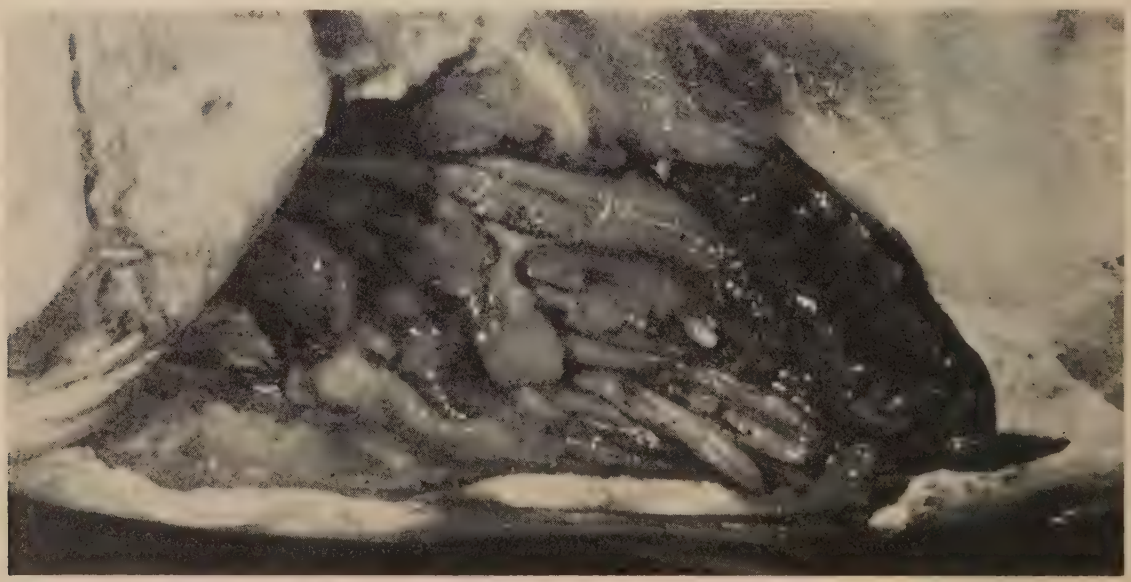

Figure 2 (b). A larval cestode (Trypanorhyncha) encysted in the mesenteries of a redfish.

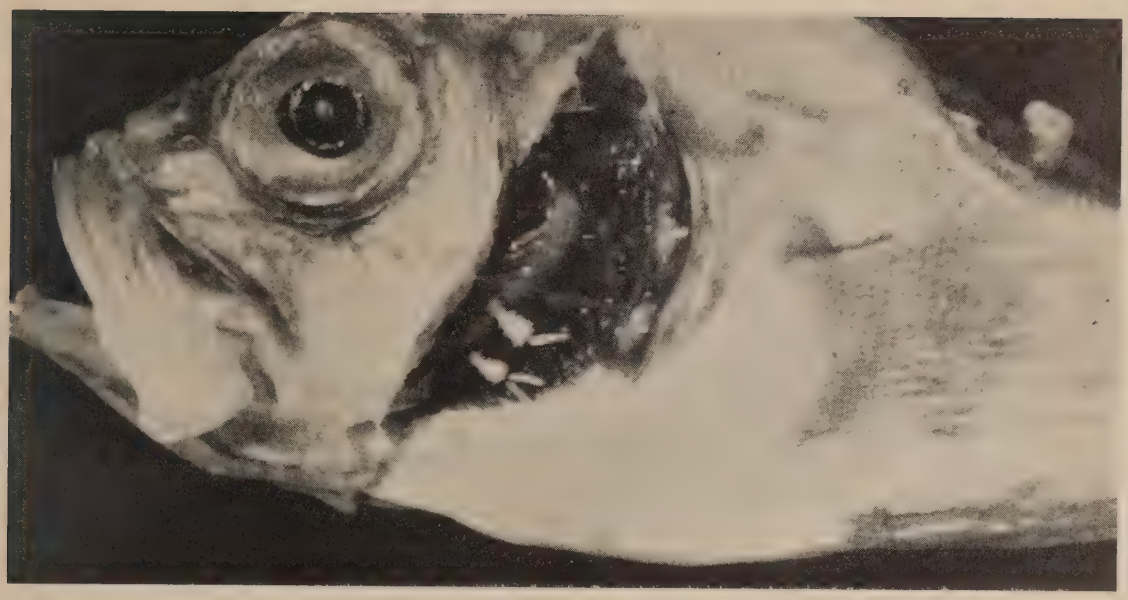

Figure 2 (c). Parasitic copepods (*Chondracanthopsis nodosus*) on the exposed gills of a redfish.

(2) that the parasite will not kill its host; and
(3) that incidences of particular parasites in an area will remain relatively stable for several years, or at least will not fluctuate widely from one year to the next.

Experimental and ecological studies therefore should be a part of any attempt to use parasitological tags, in order to be certain that the above criteria are fulfilled by each parasite studied.

In some cases the absence of a parasite in an area gives a strong indication of the extent of possible intermixing of fish from adjacent areas. For example, in our data, larval cestodes (Trypanorhyncha) were absent from Grand Banks and Gulf of St. Lawrence redfish samples, but were abundant in all other areas. This discontinuity could only be maintained by lack of any effective movement of fish from areas where the parasite occurs to the Grand Banks or the Gulf of St. Lawrence. Also, the localization of the copepod *Sphyrion* in the Gulf of Maine and its virtual absence in adjacent areas preclude any extensive movement of redfish so parasitized out of the Gulf.

Usually, however, the situation is not so definitive. Most parasites occur throughout the host range, but in widely varying abundance. In this situation determination of average incidences in each area for several parasites can provide a maximum estimate of intermixing. For example, redfish from Western Bank have almost twice as many gill copepods as fish from the adjacent Roseway Bank, but only one-seventh the numbers of larval nematodes. This suggests that maximum possible interchange between these two areas is slight, otherwise greater homogeneity would exist. It is, therefore, the *composite* of frequencies of several parasites that characterizes fish from a geographic area and that may be compared with composites from other areas to obtain an indication of maximum possible intermixing. For example, comparing parasite incidences in Roseway, Western, and Grand Banks samples (Figure 3) the maximum possible interchange could be determined mathematically.

Parasite frequencies, then, can provide a means of estimating or calculating maximum *possible* movement, but the *actual* movement may be much less. As is true of most methods for the study of marine fishes, a parasitological study by itself would rarely produce definitive answers to population and migration problems. However, when parasitological data are combined with information derived from other methods of study, a significant contribution may be made.

Conclusions

(1) A survey has been made of the frequencies of five redfish parasites from the western North Atlantic. Parasites were selected for use as "natural tags" because they were relatively permanent, easily visible, and varied in abundance on different fishing grounds.

(2) Fish from each of the major fishing grounds

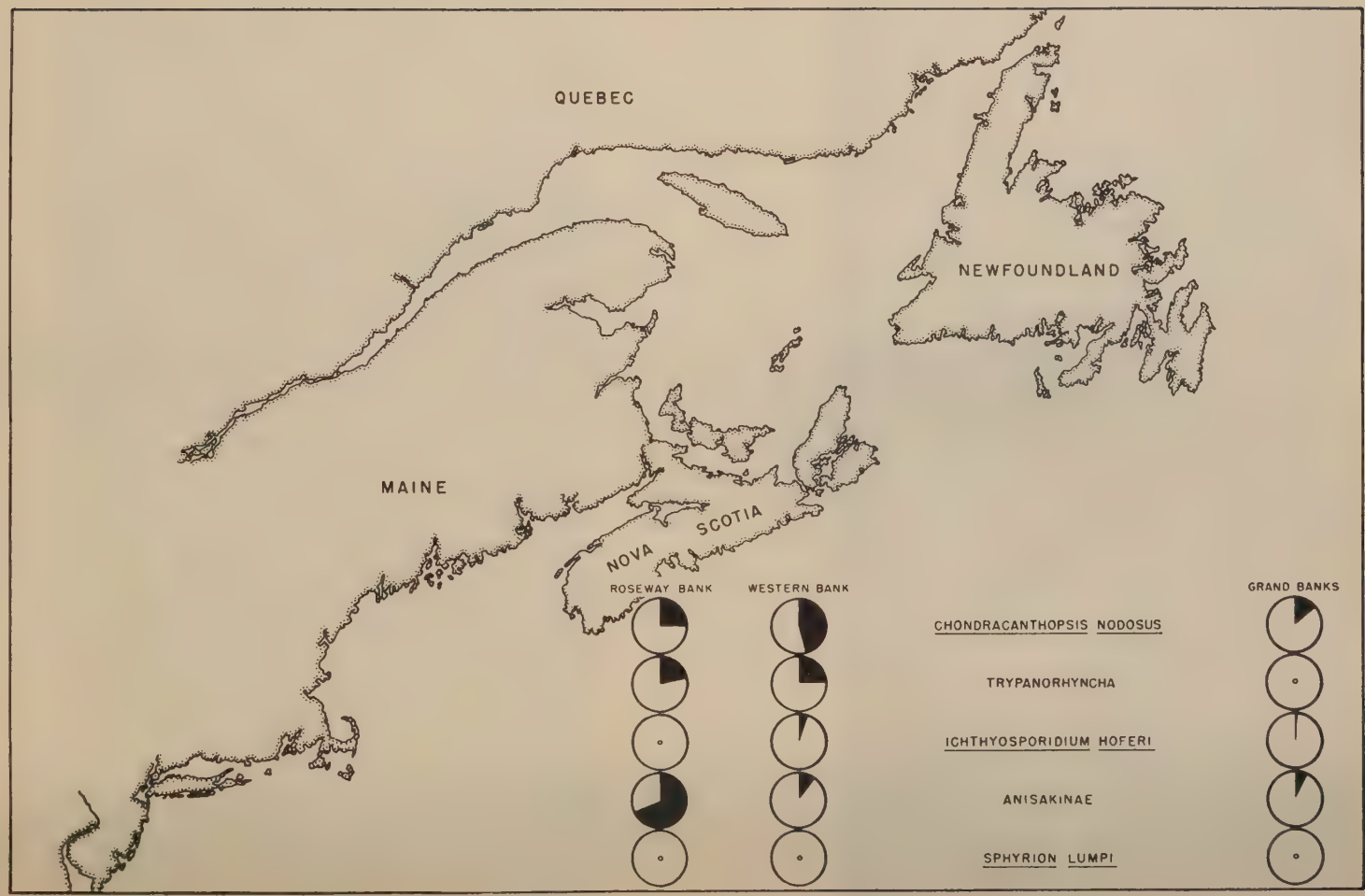

Figure 3. Incidences of five parasite tags in redfish samples from Roseway, Western, and Grand Banks.

were characterized by a composite of frequencies of all parasites. Samples from each area were distinguishable parasitologically from those of any other area.

(3) The discontinuous distribution of a larval cestode indicated that Grand Banks redfish stocks receive no contribution of adults from stocks to the westward. Localization of an ectoparasitic copepod in the Gulf of Maine indicated that the fish populations on more eastern grounds receive no contribution from the Gulf of Maine.

(4) Composite parasite frequencies of adjacent redfish stocks in and near the Gulf of Maine suggest that maximum possible intermixing is slight, even for those stocks not widely separated geographically.

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A/S L. Ihrich, Copenhagen

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CARL J. SINDERMANN, U. S. Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine. Isoagglutination in elasmobranch fishes.

Isoantibodies are common in the blood of higher vertebrates, but have been reported infrequently in teleosts (Cushing and Durall, Amer. Nat. 91: 121-126, 1957) and not at all in elasmobranchs. That this may be due principally to insufficient study was suggested by the finding of strong isoagglutinins in spiny dogfish, *Squalus acanthias*, big skates, *Raja ocellata*, and little skates, *Raja erinacea*, from the Gulf of Maine.

Individual dogfish were found by cross matching and absorptions to possess isoagglutinins for an erythrocyte antigen present in certain other individuals. Fish that carried the antigen did not have the isoagglutinin, and most fish that lacked the antigen had the isoagglutinin. Isoantibodies were not present in sera from nearly full-term or newborn dogfish "pups," but the specific erythrocyte antigen was detectable in the blood of such early-stage dogfish by reactions with isoagglutinins in adult sera.

Sera of big and little skates also contained isoantibodies for specific erythrocyte antigens. Cross matching cells and sera of big skates indicated the existence of two antigens and their corresponding isoagglutinins. Heterologous cross matching of cells and sera from the two skate species suggested that the same or closely related antigens and antibodies were involved in the reactions.

Immunogenetic studies of these and other elasmobranchs, based in part on antigens detected by natural antibodies, offer promise as criteria in determining degree of reproductive isolation of subpopulations, and may provide information about degree of intermixing.

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CARL J. SINDERMANN, U. S. Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine. The effect of larval trematode parasites on snail migrations.

Intertidal gastropods in northern New England participate in relatively extensive seasonal migrations, moving from the upper tide zones in early winter and returning in spring. Study of two species, *Nassarius obsoletus* and *Littorina littorea*, has indicated that parasitization by larval trematodes may retard or inhibit such migrations, with important ecological consequences for host and parasite.

During a study of the avian schistosome *Austrobilharzia variglandis* (Sindermann, Ecol. 41: 785-790, 1960) it was noted that mud snails (*Nassarius*) parasitized by larval schistosomes tended to remain in the high tide zone in autumn after uninfected snails had moved offshore. This provided a source of infection for migratory birds which are the definitive hosts, but also provided a possible limiting mechanism for the parasite, by immobilizing infected snails in the progressively unfavorable environment of the high tide zone in winter.

Recent study of another trematode, *Cryptocotyle lingua*, which parasitizes *Littorina littorea*, has suggested a similar effect of parasitization on host migration. Larval trematode incidence was highest in high-tide-zone snails during late autumn and winter, after most of the summer high-tide-zone population had migrated to deeper water. Conversely, low-tide-zone incidence was highest in spring, after many snails from winter low-tide-zone aggregations had migrated to the upper tide zones. In each case the observed seasonal change in incidence could be explained by immobilization of parasitized snails.

With both species, use of painted marks to distinguish normal and parasitized snails, and monthly examinations of snail movements and trematode incidences over a two-year period, have pointed to definite influence of larval trematode parasites on host migration.

PARASITE TAGS FOR MARINE FISH

BY CARL J. SINDERMANN

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PARASITE TAGS FOR MARINE FISH

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Parasites of marine fishes as well as those of other animals often exhibit remarkable geographic variations in abundance. Differences may have environmental or physiological explanations, but regardless of their causes, such variations should prove useful to the study of fish populations and migrations. Parasites may serve as "natural tags" identifying fish from a particular area or of a particular age, and natural marks of this kind can be valuable supplements to tagging programs—in fact they may be a method of choice in studying stocks and movements of fish, particularly deepwater ones, that are difficult to tag.

Some information about populations and movements of marine fish has already been obtained through studies of parasite distribution and abundance. Parasite tags have been used with profit in studying the continental origin of high seas salmon stocks in the Pacific (Margolis, 1956). A parasitic copepod (*Sphyrion lumpi*) has provided information about the degree of discreteness of western North Atlantic redfish stocks (Templeman, 1950; Perlmutter, 1953). In European waters another parasitic copepod (*Lernaeocera branchialis*) has been used to identify inshore and offshore whiting and pollock (Sproston and Hartley, 1941). Lüling (1951) noted wide geographic variations in the abundance of larval nematodes (Anisakinae) in redfish from the Iceland area. Kabata (1957, 1959) found geographic variations in the abundance of parasitic copepods of the genera *Lernaeocera* and *Acanthochondria* on groundfish from the eastern North Atlantic.

During the past four years (1955–58), a study has been made of the distribution and abundance of parasites of sea herring (*Clupea harengus*) taken on the east coast of North America. Concurrent investigations of the life cycle and ecology of several of the parasites have also been carried out, and several reports on aspects of this work have been published (Sindermann, 1957a, 1957b). The present paper summarizes the information that parasites have provided about the movements or lack of movements of intraspecies groups of herring. Results may also be used as a baseline for the study of long-term changes in parasite abundance in this important marine fish.

The author wishes to acknowledge the assistance of Donald Mairs, Frank Perkins, Alva Farrin, and others of the staff of the Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, in collection and examination of samples. The hospitality and assistance of Alexandre Marcotte, Director, Marine Biological Station, Grande Rivière, Quebec, and Paul Montreuil, Director, Marine Biological Laboratory, Grindstone, Magdalen Islands, did much to make possible the Gulf of Saint Lawrence studies included here.

METHODS

Herring are hosts to a large menagerie of parasites, some of which occur commonly, while others are rare, and some of which are relatively permanent while others are transient. Parasites reported in this paper include only those that have been found to persist in the host for a minimum of 1 year, to be easily visible, and to have a heterogeneous geographic distribution. Four parasites satisfied these requirements: *Ichthyosporidium hoferi*, a systemic fungus parasite that produces gross nodules on the heart and liver; larval cestodes of the order Trypanorhyncha, encysted in the mesenteries; larval nematodes of the subfamily Anisakinae, from the viscera; and a myxosporidian (*Kudoa clupeidae*) which produces cysts in the body muscles. A number of interesting organisms, including *Eimeria sardinae*, a sporozoan found in the testis, *Eimeria clupearum*, a sporozoan from

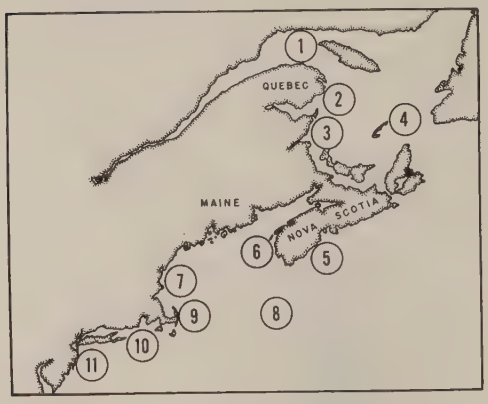

FIG. 1. Locations of sampling areas for adult herring.

the liver, and *Brachypallus crenatus*, a trematode which localizes in the stomach, were eliminated because of transiency, rarity, or inconspicuousness. Wherever possible, samples of 100 fish were examined for the 4 parasites mentioned above. Samples of adults have been grouped in the following geographic areas: (1) North Gaspe coast; (2) Chaleur Bay; (3) Northumberland Strait; (4) Magdalen Islands; (5) outer Nova Scotia coast; (6) Nova Scotia Fundy coast; (7) southern Gulf of Maine coast; (8) Georges Bank; (9) Cape Cod coast; (10) Block Island Sound; (11) New Jersey coast. Locations of these areas are shown in Fig. 1. In most cases, samples of adult herring were drawn annually during the period 1955–58 from spawning aggregations, although, because of local peculiarities of the fishery, some were taken at other times of the year. Samples of immature herring were taken during the study period from commercial catches and from experimental fishing catches along the Maine and New Brunswick coasts.

PARASITE TAGS FOR ADULT HERRING

Three parasites, all of which persist in the host for extended periods, have proved instructive, in that quantitative differences in their frequency of occurrence characterize adult herring from different geographic areas (Table 1). Percentages represent averages of many individual samples taken yearly from 1955 through 1958.

The first, a fungus parasite (*Ichthyosporidium hoferi*), has aroused interest because of its probable role in determining herring abundance. Acute infections are usually fatal within 1 month, but the chronic form of the disease has been found experimentally to persist for 18 months in some individuals. Infections reached epizootic proportions in the Gulf of St. Lawrence during the period 1954–56 and have declined rapidly since that time. The 1955–58 averages for that gulf thus include an outbreak peak and 2 years of declining incidence. The abundance of infections in Gulf of St. Lawrence herring contrasted with the very low incidence in the Gulf of Maine

TABLE 1.—AVERAGE PARASITE INCIDENCES IN ADULT HERRING, 1955–58

Area	Number of Samples	Number of Fish	Fungus (*Ichthyosporidium hoferi*) (percent)	Larval Cestodes (Trypanorhyncha)[1] (percent)	Larval Nematodes (Anisakinae)[1] (percent)
North Gaspe Coast (1)	4	400	15	0	18.5
Chaleur Bay (2)	15	1350	22	0	19
Northumberland Strait (3)	6	500	13	0	31
Magdalen Islands (4)	4	500	22	0	20
Outer Nova Scotia Coast (5)	11	950	3	2	76
Nova Scotia Fundy Coast (6)	6	550	2	2	64
Southern Gulf of Maine Coast (7)	14	1650	1	6	27
Georges Bank (8)	8	900	1	13	30
Cape Cod (9)	7	550	1	19	21
Block Island Sound (10)	4	400	1	46	12
New Jersey Coast (11)	4	400	1	31	14

[1] Further identification of these larval worms is difficult without experimental rearing of adults.

herring throughout the study period—a highly improbable situation if effective intermixing of fish from the two gulfs occurred. Examination of all available published data on the disease in western North Atlantic herring has disclosed evidence for periodic but not simultaneous outbreaks in both gulfs (Fig. 2), suggesting possible oscillation in abundance between the two areas.

Abundance of larval cestodes (order Trypanorhyncha) complemented fungus incidence, in that infections decreased with increasing latitude. The cestodes were abundant in the southern Gulf of Maine, but were not found in 4 years of sampling in the Gulf of St. Lawrence. Unlike the fungus organism, cestode abundance in particular regions remained remarkably constant throughout the survey period. Heterogeneity of fungus and cestode distribution and the reciprocal nature of this distribution indicate that there can be little if any interchange of adult fish between the two gulfs.

Larval nematodes of the subfamily Anisakinae were more abundant in Nova Scotia samples than in those from the Gulf of St. Lawrence or Georges Bank. As with larval cestodes, incidence of nematodes remained relatively constant in most regions during the survey period.

If each parasite frequency is considered as a separate population characteristic of herring from a particular geographic area,

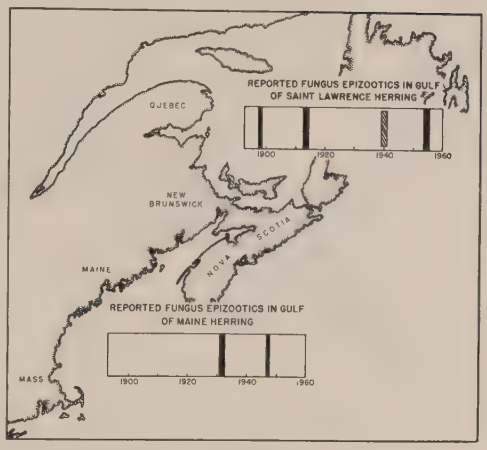

FIG. 2. Fungus (*Ichthyosporidium hoferi*) epizootics reported in herring of the Gulf of Maine and the Gulf of St. Lawrence. The Gulf of St. Lawrence outbreak which occurred about 1940 was not recorded in scientific literature, and is included here only on the strength of verbal reports from fishermen of the area.

it should be possible to achieve an approximation of maximum possible intermixing of adult herring between any two areas. Such a statistical manipulation of data must be confined to the survey period, should be limited to samples from spawning aggregations, and must assume relative permanence of the characteristics used. Within these restrictions we may conclude that intermixing of Gulf of Maine and Gulf of St. Lawrence adult herring approaches zero, and that

FIG. 3. Myxosporidian (*Kudoa clupeidae*) cysts in the flesh of 1-year-old herring.

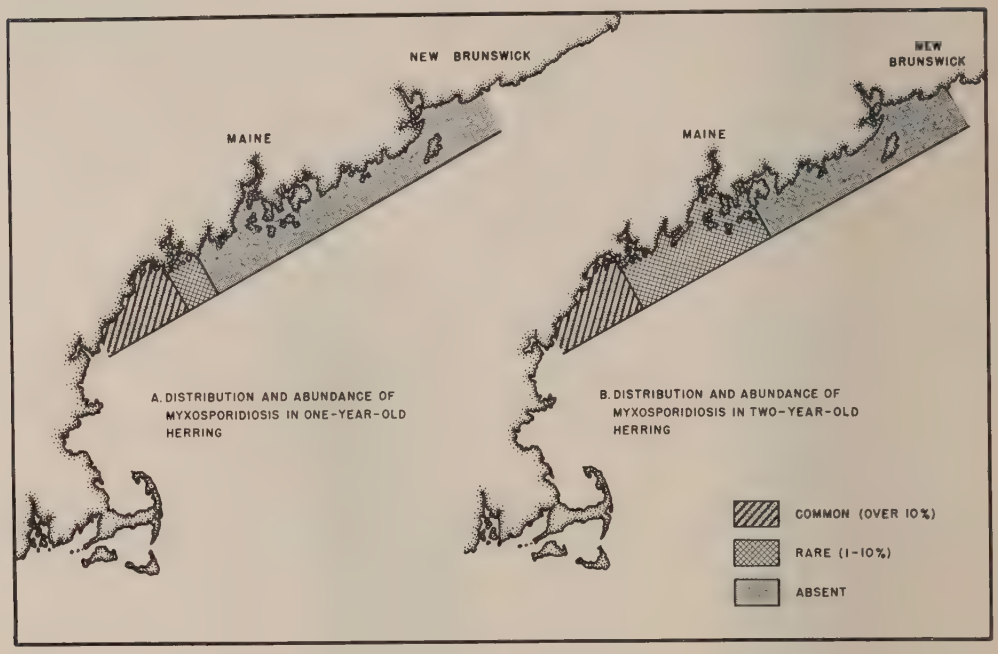

FIG. 4. (a).—Distribution of the myxosporidian *Kudoa clupeidae* in 1-year-old fish. (b).—Distribution of the myxosporidian in herring almost 2 years old.

only limited exchange between Nova Scotia and Georges Bank spawning aggregations could occur.

This, of course, is not genetic information, and tells us little of the true population structure of the species. It can, however, supply information about movements of adults, which should be a valuable supplement to population studies.

PARASITE TAGS FOR IMMATURE HERRING

Interest in movements of immature herring is derived primarily from the fact that the Gulf of Maine sardine-herring fishery concentrates almost entirely on 1- and 2-year-old fish. It is therefore important to understand as much as possible about movements of such herring during their brief period of economic importance. Also, considering possible future management of this species, knowledge of the homogeneity or heterogeneity of the stocks is necessary.

Two parasites have provided information about movements of sardine-size herring. The first, a myxosporidian (*Kudoa clupeidae*), comes close to being an ideal "natural tag" for such fish. It is easily visible (Fig. 3), is acquired early in the first year of life of the host, persists for at least 2 years, does not cause differential mortality, and, most importantly, is distributed discontinuously in immature Gulf of Maine herring. Infections in 1-year-old fish have been found only along the western Maine coast (Fig. 4a). When fish of the same year class were sampled almost a year later, infections were found only as far east as Mount Desert Island (Fig. 4b), giving an exact picture of limited eastward movement during the intervening period. Study of myxosporidian distribution in two year classes (1954 and 1955) gave comparable results. Seasonal examination of the distribution of this parasite in 1957–58 provided an even more precise picture of just when the limited movements occurred (Fig. 5).

Larval nematodes (Anisakinae), already discussed as "natural marks" for adult her-

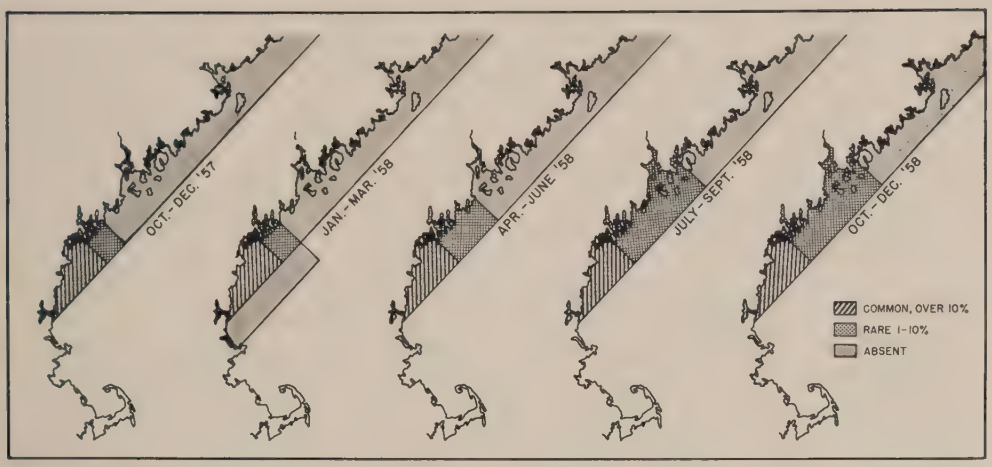

FIG. 5. Distribution of the myxosporidian in herring of the 1956 year class, sampled every 3 months during the period when its members were economically important as sardines.

ring, have complemented the picture of myxosporidian distribution. Examination of the same samples used for the myxosporidian study in 1955 and 1956 disclosed that larval nematodes were more numerous in 1-year-old fish from eastern Maine than in those from western Maine. Examination of fish of the same year classes almost a year later disclosed the persistence of greater numbers of worms in herring from eastern Maine. Incidences in the 2-year-old fish from both areas were higher than in 1-year-olds, with "western" fish showing a proportionally greater increase in worm incidence than "eastern" fish (Fig. 6). If it is assumed that there is a constant increase in numbers of worms with age in each area if no movement occurs, the data suggest that some of the more heavily parasitized eastern herring could have moved westward during the intervening period. Although other factors may be important, this could account for the disproportionate rise in worm incidence in western fish.

In summary, myxosporidian and nematode incidences indicating little eastward movement of herring that had spent their first year of life west of Penobscot Bay, but possibly greater westward movement of fish that had spent their first year east of that bay. For the 1954 and 1955 year classes, incidences of myxosporidian infections in western 2-year-old fish were only slightly over half those found in 1-year-old fish (Sindermann, 1957b), while nematode incidences in western 2-year-olds increased disproportionately over those found in 1-year-olds, when compared with their eastern counterparts. Both these findings suggest possible movement of eastern fish westward during their second year of life,

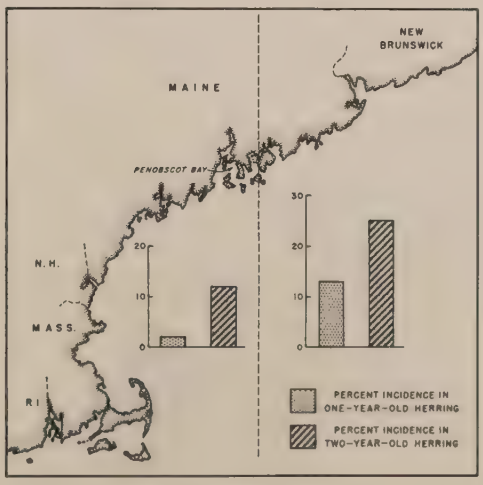

FIG. 6. Incidence of larval nematodes in 1- and 2-year-old herring from the eastern and western Maine coast.

but myxosporidian distribution alone precludes any major eastward movement during the period. It is also possible that long-term changes in the pattern of movements could occur, and that a continuing examination of nematode and myxosporidian incidences in each year class would provide some indication of this.

DISCUSSION

Studies of fish populations and migrations, of great importance to intelligent manipulation of marine resources, have been based traditionally on tagging and morphological characteristics. It seems reasonable that the greater the number of criteria used, the closer to reality will the conclusions become. The research summarized in this paper was designed to assess the value of parasites as "natural tags" for population and migration studies. There are, of course, many difficulties inherent in the use of parasites as tags. They may provide little information about extremely local movements of fish. Also, information about the duration of the parasite in the fish host must be available, as well as some knowledge of infection rates.

On the other hand, parasitological examination of a commercial marine fish species for the existence of "natural marks" may have certain advantages over an extensive tagging program. The primary advantage is one of lower cost, since tagging programs are expensive, while parasite studies may be made with samples from the commercial fishery, and need not involve vessel time—often the principal consumer of research funds. Examination of parasite distribution may also make a real contribution by furnishing advance clues about fish movements, which may be exploited in later tagging programs. Attempts to tag deepwater fishes such as the Atlantic redfish (*Sebastes marinus*) in their deepwater environment have not been successful; parasite tags should be of particular value to such investigations, and some insights have already been gained through this method (Templeman, 1950; Perlmutter, 1953; Sindermann, in press).

In some cases the absence of a parasite in an area may indicate lack of intermixing of fish from adjacent areas. For example, in our data, larval cestodes (Trypanorhyncha) were absent from Gulf of St. Lawrence herring samples, but were abundant in the southern Gulf of Maine samples. This discontinuity could only be maintained by lack of any effective movement of fish to the Gulf of St. Lawrence from areas where the parasite occurs. Usually, however, the situation is not as definitive. Most parasites occur throughout the host range, but in widely varying abundance. In this case, determination of average incidences in each area for several parasites can provide a maximum estimate of intermixing. For example, herring spawning on the coast of Nova Scotia had more than twice the numbers of larval nematodes of fish spawning on Georges Bank, but less than one-fifth the numbers of larval cestodes. This suggests that maximum possible interchange of adults between these two areas is slight, otherwise greater homogeneity would exist. It is therefore the composite of frequencies of several parasites that characterizes fish from a geographic area, and that may be compared with composites from other areas to obtain an indication of maximum possible intermixing.

Parasite frequencies, then, can provide a means of estimating or calculating maximum possible movement, but the actual movement may be much less. As is true of most methods for the study of marine fish, a parasitological study by itself would rarely produce definitive answers to population and migration problems. However, when parasitological data are combined with information gained from the use of other techniques, such as tagging and meristic studies, a significant contribution may be made.

It seems pertinent to this consideration that a concurrent serological study of herring, particularly of erythrocyte antigens, has provided support for some of the conclusions from parasitological data (Sindermann and Mairs, 1959). Quantitative differences in frequencies of fish with certain blood types have pointed to the existence

of two subgroups of immature herring, with a transition zone in the vicinity of Mount Desert Island—a finding which parallels the parasitological results reported here. This tends to increase confidence in evidence from parasitology, although the ultimate test must lie in agreement or lack of agreement with conclusions drawn from the use of established criteria for population and migration studies.

SUMMARY

A study of parasite distribution and abundance in immature and adult sea herring was carried on from 1955 through 1958 to provide information about intraspecies groups and their movements. Lack of intermixing or interchange of adult herring from the Gulf of Maine and the Gulf of St. Lawrence was indicated by larval cestode and fungus incidences. Within the Gulf of Maine, herring spawning on Georges Bank were distinguishable from Nova Scotia spawners on the basis of quantitative and reciprocal differences in frequencies of larval nematode and cestode parasites. The distribution of two parasites—a myxosporidian (*Kudoa clupeidae*) and larval nematodes (Anisakinae)—in immature herring from the Gulf of Maine demonstrated the existence of two parasitologically recognizable groups and the lack of major migrations of such fish.

Examination of parasite distribution and abundance thus constitutes another technique, along with the more established methods of tagging and morphological examination, of possible value in assessing the degree of discreteness of marine fish populations and in determining movements or lack of movements of fish.

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A BLOOD GROUP SYSTEM FOR SPINY DOGFISH, SQUALUS ACANTHIAS L.

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Recent expansion of interest in fish immunogenetics, particularly in blood group antigens (Cushing and Durall, 1957; Ridgway, Cushing and Durall, 1958; Suzuki, Shimizu and Morio, 1958; Sindermann and Mairs, 1959; Ridgway and Klontz, 1960), has resulted in description of antigen systems for tuna and herring, and in quantitative information about antigen frequencies in populations of herring, tuna and salmon. The elasmobranch fishes have not been examined thus far, but it seems quite possible that serological methods of population and migration study could be of particular value to investigations of certain shark species. The recognition and description of blood group antigens, and where possible the genetic systems that determine their occurrence, are preludes to quantitative determinations of antigen and gene frequencies in populations. As an exploratory step in such studies of sharks, and as part of a general immunogenetic investigation of marine organisms, this report is concerned with isoagglutinins and erythrocyte antigens of the spiny dogfish, *Squalus acanthias* L. Included are serological approaches and data supporting the proposal of a first blood group system—the "S" system—for this species.

Materials and Methods

Dogfish were obtained from several places in the Gulf of Maine (Georges Bank, Casco Bay, Sheepscot Bay and Muscongus Bay) and were bled by puncturing the heart or by severing the caudal artery. Serum was decanted after overnight expression at 4° C. and inactivated at 50° C. for 30 minutes to destroy complement. Cells were washed three times in 1.5% saline and used in approximately 4% suspensions in 1.5% saline. Cross-reactions among dogfish sera and cells were tested by tube agglutination with .2 ml. undiluted serum and .05 ml. cell suspension. Tubes were read after 30-minute incubation at room temperature. Presence and degree of agglutination were recorded conventionally with the following symbols: ++++, complete agglutination with a single consolidated pellet; +++, strong agglutination with several large clumps; ++, moderate agglutination with numerous smaller clumps; +, weak agglutination with many very small clumps visible macroscopically; −, no agglutination. Saline controls were used throughout, and critical tests repeated. Absorptions of dogfish sera—which may remove certain antibodies selectively—involved addition of undiluted serum from one fish to packed washed cells from another fish in 1 : 1 proportions. The cell-serum sus-

[1] The authors would like to acknowledge the technical assistance of Alva Farrin, U. S. Bureau of Commercial Fisheries, Boothbay Harbor, Maine. The Casco Bay dogfish-processing laboratory of Wards Natural Science Establishment, and the Maine Department of Sea and Shore Fisheries cooperated in obtaining some of the blood samples used in this study.

pension was incubated 10 minutes at room temperature, centrifuged, and the absorbed serum decanted and used in cell agglutination tests. One such absorption was sufficient to remove all antibodies reactive with the absorbing cells but in some cases left antibodies for cells from other fish.

Rabbit antisera were produced by 6 subcutaneous injections of 1 ml. washed dogfish cells given on alternate days. The rabbits were bled terminally 10 days after the last injection, and the antisera frozen in 3-ml. aliquots until used. Antisera were inactivated at 56° C. for 30 minutes just before testing, to destroy complement. Tests by tube agglutination used .2 ml. diluted antiserum and .05 ml. cell suspension. Readings were taken after 15-minute incubation at room temperature and 30-second centrifugation. Presence and degree of agglutination were recorded as described above. Antiserum absorptions, which constitute a fractionation method to produce specific reagents, involved addition of antiserum (diluted 1:2 with 1.5% saline) to packed washed cells from individual dogfish in proportions of 1 part cells to 4 parts antiserum. The cell-antiserum suspension was incubated 10 minutes at room temperature, centrifuged, and the absorbed antiserum decanted and tested at 1:4 dilution. One such absorption was sufficient to remove all antibodies reacting with the absorbing cells but in some cases left antibodies capable of reacting with cells from other individuals.

Dogfish donors and recipients used in isoimmunizations were tagged and maintained in sea-water tanks of the U. S. Bureau of Commercial Fisheries Biological Laboratory at Boothbay Harbor. The fish were trial bled by heart puncture; cross-reactions and tests with rabbit antisera were carried out on the samples obtained. Results of these tests determined the nature of the subsequent immunizations attempted. Recipient dogfish received 2 ml. of cells bled from the donor weekly and washed three times before injections, which were alternately intraperitoneal and intracardial. Trial bleedings for isoimmune antibodies were made two weeks following the fourth injection.

Dogfish embryos (15–23 cm.) used in the comparative study of erythrocyte antigens were obtained by dissections of gravid females or were aborted by such females after capture. They were bled by severing the caudal artery or by heart incision and tested with the same methods used for adults.

Results

1. *Isoagglutination*

Cross-matching of cells and undiluted sera from 20 individuals gave the first clear indication of individual antigenic differences in dogfish, as seen in Table I. Sera from fish numbered 5, 6, 9, 12, 15, 16 and 17 contained isoantibodies (isoagglutinins) that reacted with cells of fish numbered 1, 2, 3, 4, 7, 8, 10, 11, 13, 14, 18, 19 and 20. Sera from fish whose cells were agglutinated did not contain antibodies for any of the cells tested. Conversely, cells from fish whose serum contained the agglutinins did not possess antigens reacting with any of the sera tested. The average isoagglutinin titer of the sera tested was 4.

The simplest explanation for the observed results was that the positive cells contained an antigen (tentatively labelled "antigen S") which negative cells lacked and that agglutinating sera contained a specific "anti-S" agglutinin for the antigen.

TABLE I

Cross-reactions of sera and cells from 20 dogfish

Serum \ Cells	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
2	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
3	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
4	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
5	+++	++++	+++	+++	−	−	++	+++	−	++++	+++	−	++++	+++	−	−	−	+++	++++	++++
6	+++	++++	+++	++++	−	−	+++	+++	−	++++	+++	−	+++	+++	−	−	−	+++	++++	++++
7	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
8	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
9	++	+++	+++	+++	−	−	++++	++	−	+++	+++	−	+++	+++	−	−	−	++	+++	++++
10	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
11	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
12	+++	+++	++++	+++	−	−	+++	+++	−	+++	+++	−	+++	+++	−	−	−	+++	+++	+++
13	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
14	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
15	+++	++++	+++	++	−	−	++++	+++	−	+++	+++	−	++++	++	−	−	−	+++	++++	++++
16	+++	+++	++++	+++	−	−	++++	+++	−	+++	+++	−	++++	++	−	−	−	+++	+++	++++
17	+++	+++	+++	+++	−	−	++++	+++	−	++++	+++	−	++++	+++	−	−	−	+++	+++	++++
18	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
20	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−

Validity of this explanation was supported by absorptions of sera containing anti-S agglutinins with positive and negative cells, and by an absorption analysis of a single serum, as illustrated in Table II.

Absorptions with cells lacking antigen S did not remove any antibodies, while absorptions with cells carrying antigen S removed all antibodies, not only for themselves, but for all other positive cells as well. This is strong evidence that the antigens involved are identical, or at least very nearly so. Sera containing the anti-S agglutinin were pooled as a test reagent (Reagent 1) for quantitative studies of

TABLE II

Results of absorption of dogfish isoantibodies by dogfish cells

Serum	Absorbed with cells of	Cells tested									
		1	2	5	6	9	16	17	18	19	20
5	1	–	–	–	–	–	–	–	–	–	–
5	2	–	–	–	–	–	–	–	–	–	–
5	5	+++	+++	–	–	–	–	–	+++	++++	+++
5	6	+++	++++	–	–	–	–	–	+++	+++	+++
5	9	+++	+++	–	–	–	–	–	++++	++	+++
5	16	+++	+++	–	–	–	–	–	+++	+++	++++
5	17	+++	++	–	–	–	–	–	++	+++	+++
5	18	–	–	–	–	–	–	–	–	–	–
5	19	–	–	–	–	–	–	–	–	–	–
5	20	–	–	–	–	–	–	–	–	–	–
6	5	+++	++++	–	–	–	–	–	++	+++	+++
6	1	–	–	–	–	–	–	–	–	–	–
9	2	–	–	–	–	–	–	–	–	–	–
12	9	+++	+++	–	–	–	–	–	++	+++	+++
15	17	+++	++++	–	–	–	–	–	+++	++++	++
16	18	–	–	–	–	–	–	–	–	–	–
17	5	+++	++	–	–	–	–	–	+++	++++	++++
18	2	–	–	–	–	–	–	–	–	–	–
18	16	–	–	–	–	–	–	–	–	–	–

S-antigen frequencies, as were sera lacking the anti-S agglutinin (Reagent 2). All subsequent samples were tested with the reagents and were also cross-matched in groups of 10 or 20, since it was not possible to keep cells for longer than one week without freezing or other treatment.

2. *Antiserum absorptions*

Further elucidation of the antigen system disclosed by isoagglutination was obtained by absorption analysis of a rabbit anti-dogfish serum (BHD64R). The rabbit had been immunized with washed cells from a single dogfish found in preliminary tests to possess antigen S. The antibody content of the normal serum of this rabbit before immunization was not determined, but the titer of the unabsorbed antiserum was 128. Results of absorptions of this antiserum with cells of the same dogfish used in the isoagglutination study are illustrated in Table III.

Absorption with cells of 5, 6, 9 and 12, already found to lack reactive antigens

in cross-matching tests, removed species antibodies—those which indiscriminately agglutinate cells of all individuals—but left antibodies which agglutinated cells of 1, 2, 3, 4, 7, 8, 10 and 11. Results of tests with the absorbed antiserum agreed with those obtained in the isoagglutinin study, cells of individuals 1, 2, 3, 4, 7, 8, 10, and 11 carrying an antigen not occurring on cells of individuals 5, 6, 9, and 12. The absorptions further disclosed a second antigen on the cells of fish number 2 that was not detected by isoantibodies in dogfish sera. Absorption of the rabbit antiserum with cells of dogfish number 2 removed antibodies for all other cells, while absorption with cells of 1, 3, 4, 7, 8, 10 and 11 removed antibodies for all others except those of fish number 2. For descriptive purposes the antigens detected by absorbed rabbit antiserum have been labelled "S_1" and "S_2"—S_1 being identical to the antigen detected by isoagglutination. Both antigens were reactive with the reagent prepared by pooling antiserum absorbed by cells of 5, 6, 9, and

TABLE III

Results of absorpiions of rabbit anti-dogfish serum by dogfish cells

Antiserum BHD64R absorbed with cells of dogfish:	Test cells											
	1	2	3	4	5	6	7	8	9	10	11	12
1	−	++	−	−	−	−	−	−	−	−	−	−
2	−	−	−	−	−	−	−	−	−	−	−	−
3	−	++	−	−	−	−	−	−	−	−	−	−
4	−	++	−	−	−	−	−	−	−	−	−	−
5	+	++	+	+	−	−	+	+	−	+	+	−
6	+	++	+	+	−	−	+	+	−	+	+	−
7	−	++	−	−	−	−	−	−	−	−	−	−
8	−	++	−	−	−	−	−	−	−	−	−	−
9	+	++	+	+	−	−	+	+	−	+	+	−
10	−	++	−	−	−	−	−	−	−	−	−	−
11	−	++	−	−	−	−	−	−	−	−	−	−
12	+	++	+	+	−	−	+	+	−	+	+	−
Unabsorbed	+++	+++	+++	++++	++	++	++++	++++	+++	++++	+++	++

12 (Reagent 3), and S_2 was reactive with the reagent prepared by pooling antiserum absorbed with cells of 1, 3, 4, 7, 8, 10 and 11 (Reagent 4). Antiserum absorbed with cells of fish number 2 constituted a negative control reagent (Reagent 5).

According to the reactions obtained, fish number 2 possessed antigens S_1 and S_2, fish number 1, 3, 4, 7, 8, 10 and 11 possessed antigen S_1, and fish number 5, 6, 9 and 12 lacked both antigens.

3. *Definition of reagents*

The results of isoagglutinations and antisera absorptions presented in previous sections show that it is possible to define five reagents for the detection of antigenic specificities S_1 and S_2.

(1) Dogfish serum containing anti-S agglutinins specific for S_1 antigen.
(2) Dogfish serum from S_1 positive fish lacking anti-S agglutinins—a negative control.
(3) Absorbed rabbit anti-dogfish serum (BHD64R) containing antibodies specific for S_1 and S_2 antigens.

TABLE IV

*Dogfish isoagglutination and antiserum absorptions**

Reagent:	Test cells									
	21 (S_0)	22 (S_1)	23 (S_1)	24 (S_0)	25 (S_1)	26 (S_1)	27 (S_1)	28 (S_2)	29 (S_1)	30 (S_1)
(1) Dogfish anti-S_1	–	++++	+++	–	++++	++++	+++	–	++++	++++
(2) Dogfish negative	–	–	–	–	–	–	–	–	–	–
(3) Rabbit anti-S_1 & S_2	–	+++	++	–	++	+	++	++	+	++
(4) Rabbit anti-S_2	–	–	–	–	–	–	–	++	–	–
(5) Rabbit negative	–	–	–	–	–	–	–	–	–	–
Serum of Dogfish No.										
21 (anti-S_1)	–	+++	+	–	++	++	+	–	++	+++
22 (–)	–	–	–	–	–	–	–	–	–	–
23 (–)	–	–	–	–	–	–	–	–	–	–
24 (anti-S_1)	–	++++	++	–	++	++	++++	–	++	++
25 (–)	–	–	–	–	–	–	–	–	–	–
26 (–)	–	–	–	–	–	–	–	–	–	–
27 (–)	–	–	–	–	–	–	–	–	–	–
28 (anti-S_1)	–	++++	++++	–	+++	++++	++++	–	++++	+++
29 (–)	–	–	–	–	–	–	–	–	–	–
30 (–)	–	–	–	–	–	–	–	–	–	–
Antiserum BHD64R absorbed with cells of dogfish										
21 (S_0)	–	+	++	–	+	++	+	+	++	+
22 (S_1)	–	–	–	–	–	–	–	++	–	–
23 (S_1)	–	–	–	–	–	–	–	++	–	–
24 (S_0)	–	+	+	–	+	+	+	++	+	+
25 (S_1)	–	–	–	–	–	–	–	++	–	–
26 (S_1)	–	–	–	–	–	–	–	++	–	–
27 (S_1)	–	–	–	–	–	–	–	+	–	–
28 (S_2)	–	+	++	–	++	++	++	–	++	+
29 (S_1)	–	–	–	–	–	–	–	+	–	–
30 (S_1)	–	–	–	–	–	–	–	+	–	–
Unabsorbed	++	++++	+++	+++	++++	++++	+++	++++	+++	+++

* Erythrocyte antigens of each fish, as disclosed by this analysis, are in parentheses after each test cell number.

(4) Absorbed rabbit anti-dogfish serum (BHD64R) containing antibodies specific for S_2 antigen.
(5) Absorbed rabbit anti-dogfish serum (BHD64R) lacking antibodies for S_1 and S_2—a negative control.

The reality of the two antigens in the system and the specificity of the reagents for their detection were clearly demonstrated with a second series of samples tested first with the five reagents, then examined for isoagglutination, and finally analyzed by antiserum absorption, as seen in Table IV.

From this analysis, dogfish 22, 23, 25, 26, 27, 29 and 30 possessed S_1 antigen, 28 possessed S_2 antigen, 21 and 24 lacked either antigen, and none had both antigens. The antiserum absorptions provided a sixth reagent (absorbed with S_2 cells of 28) that was specific for cells containing S_1 antigen—completing the battery of reagents prepared from antiserum BHD64R necessary for detection of both S_1 and S_2 in quantitative studies of antigen frequencies. Subsequent samples, totalling 138, were tested with all six reagents. Dogfish 28 was the only one found to carry only antigen S_2.

4. *Isoimmunization attempts*

A further analysis of the erythrocyte antigens of individual dogfish was attempted with isoimmunization—injecting the cells of one fish into another fish. Dogfish in the series 21 to 30 described in the previous section and already characterized according to S antigens, were tagged and maintained in the sea-water tanks of the U. S. Bureau of Commercial Fisheries Biological Laboratory at Boothbay Harbor and were used in isoimmunization attempts, according to the following experimental design:

(1) dogfish 21, which lacked S_1 antigen and contained isoagglutinins for S_1, was injected with washed cells of 30 which possessed S_1;
(2) dogfish 25, which possessed S_1 antigen and lacked isoagglutinins for S_1, was injected with cells of 22, which possessed S_1; and
(3) dogfish 26 which possessed S_1 antigen and lacked isoagglutinins for S_1, was injected with cells of 24, which lacked S_1.

Two weeks after the final injection, sera from the three recipient dogfish were tested against cells of donors, and against cells of other dogfish in the series 21 to 30.

No change in agglutinin titer or specificity of dogfish sera was found after the isoimmunization attempts. Only the reactions of antigen S_1 were tested, since the single S_2 dogfish (number 28) died shortly after the first test bleeding. Under the conditions of the experiment (four weekly injections, tests two weeks after the last injection, sea-water temperature 12–17° C.) injection of S_1 cells into a recipient lacking S_1 caused no increase in anti-S_1 agglutinin titer. Injection of S_0 cells into a S_1 individual did not produce anti-S_0 agglutinins. Further isoimmunizations should be attempted with dogfish possessing S_2 and other antigens, possibly extending over a greater period of time or involving more frequent injections.

5. *Comparison of erythrocyte antigens of gravid females and embryos*

Since the spiny dogfish is an ovoviviparous species, it was possible to obtain presumptive genetic information about the S blood groups by comparing erythrocyte

antigens of females and their well-developed embryos ("pups"). Detectable isoantibodies were not present in sera of nearly full-term pups, but erythrocyte antigens—agglutinated by isoantibodies in sera from adult dogfish and by absorbed antiserum—gave reactions of the same specificity and intensity as those of adult dogfish. Blood groups of females and their progeny are presented in Table V. Females with blood group S_1 had S_1S_2, S_1 and S_0 pups, while females with blood group S_0 had S_0 and S_1 pups.

TABLE V

Blood groups of gravid female dogfish and their unborn progeny

Blood group of mother	Blood group of embryos
(1) S_1	S_1, S_1, S_1, S_1, S_0
(2) S_0	S_1, S_1, S_1, S_1, S_1
(3) S_1	S_1S_2, S_0, S_0
(4) S_0	S_1, S_1, S_1, S_1
(5) S_1	S_1, S_1, S_1
(6) S_0	S_1, S_0, S_0, S_0
(7) S_1	S_1, S_1, S_1, S_1, S_0
(8) S_0	S_1, S_1, S_0, S_0, S_0, S_0, S_0, S_0
(9) S_1	S_1, S_1, S_1, S_1
(10) S_0	S_0, S_0, S_0, S_0, S_0
(11) S_1	S_1, S_1
(12) S_1	S_1, S_1, S_1, S_1, S_1, S_0

6. *The S blood group system of dogfish*

Although further genetic evidence—preferably based on results of known crosses—is necessary, the S blood group system can be proposed tentatively. Based on (1) results of isoagglutinations, antiserum absorptions and isoimmunization attempts; (2) comparisons of maternal blood groups with those of unborn pups; and (3) analyses of 138 individual dogfish blood samples from different Gulf of Maine areas with the six reagents described earlier, the following statements can be made:

(1) The S blood group system of spiny dogfish, *Squalus acanthias,* contains at least two antigens, S_1 and S_2, that may or may not be possessed by individual fish.

(2) Isoantibodies present in sera of most dogfish whose cells lack S_1 antigen will agglutinate cells possessing only S_1. Isoagglutinins for S_2 antigens have not been detected.

(3) Antigen S_1 can be demonstrated with antibodies remaining in rabbit antiserum after absorption by cells of dogfish containing S_2 antigen, and antigen S_2 with antibodies remaining after absorption by S_1 cells. Cells not agglutinated by either absorbed antiserum have been designated S_0. Thus far an anti-S_0 serum has not been found.

(4) Individual fish may possess both, either, or neither of the antigens, so possible blood groups (types) are S_1S_2, S_1, S_2, and S_0.

(5) Of the 138 dogfish tested thus far from the Gulf of Maine, two individuals had S_1S_2 blood group, 92 had S_1, 1 had S_2 and 43 had S_0.

Discussion

The present paper demonstrates individual differences in erythrocyte antigens and an isoantibody system in a species of the elasmobranch fishes. A clearly defined antigen system, demonstrable with isoagglutinins and absorbed rabbit antiserum, exists in spiny dogfish. The system parallels the Tg system of tuna (Suzuki, Shimizu and Morio, 1958) in that it is composed of two antigens, with individuals possessing either, both or neither antigen. Similarities also exist with an isoagglutinin system described by Cushing and Durall (1957) in brown bullheads (*Ictalurus n. nebulosus*). The dogfish blood groups described here seem definitive enough in their present state to be used in quantitative studies of populations and in tracing migrations of infraspecies groups, if geographic variations in antigen frequencies exist. Thus far six individuals have been found that lacked S antigens and also lacked detectable isoagglutinins in their serum. This might be expected, since the agglutinin titers of individual sera varied considerably. As greater numbers of samples are tested, exceptions may occur, as they have been found to occur in human and other animal groups (Owen, 1954; Stormont, 1955), but the proposed system has proved remarkably specific and definitive thus far in tests of *Squalus* from the Gulf of Maine. Future studies may suggest modification of the system, just as extended studies of human blood group systems have resulted in modifications of original hypotheses (Landsteiner, 1901; von Dungern and Hirzsfeld, 1911; Friedenreich, 1936), but the reality of the dogfish S antigens described here seems clear.

Blood group systems are essentially genetic systems, and hence cannot be fully described, understood or accepted without genetic information. Any postulated classification of individual antigenic differences—such as that here proposed for dogfish—should be supported eventually by genetic evidence. It is difficult to make experimental crosses and to rear offspring of most marine fish for such studies, but the ovoviviparous species including *Squalus* can provide some interim data. Comparing blood groups of pregnant females and their unborn offspring may offer presumptive genetic evidence supporting erection of blood group systems. Such a comparison of female dogfish and their pups in the present work suggests that the S system of blood group antigens may be controlled by three alleles: S^1, S^2 and S^0. According to this explanation the S_1S_2 phenotype would have S^1S^2 genotype; S_1 would have S^1S^1 or S^1S^0; S_2 would have S^2S^2 or S^2S^0; and S_0 would have S^0S^0. Based on a three-allele hypothesis, quantitative data from the limited sample of adult dogfish presented in this paper result in the following gene frequencies: S^1—0.44, S^2—0.01, S^0—0.55. The number of individuals tested is small, so expected ideal values for the entire Gulf of Maine population may not be represented. Also, there may be local differences in frequencies, so the next logical step would be determination of antigen and gene frequencies in large samples of *Squalus* from different geographic areas. In addition to testing the genetic hypothesis, this quantitative work could provide some information about the degree of reproductive isolation of groups and the subpopulation structure of the species.

The existence of sharp individual differences in the antigenic constitution of dogfish offers the promise of comparable differences in other elasmobranch fishes. Since certain of the larger shark species are receiving increasing attention from biologists as well as from the popular press (Gilbert, 1960), immunogenetic methods

may offer a useful approach to studies of their migrations and populations. While the large sharks provide a practical stimulus for research, smaller selachians such as dogfish may actually be animals of choice in such investigations. In addition to the possession of a clearly defined isoantibody system, dogfish occur in schools, are easily handled in marine aquaria, and yield copious amounts of blood. Also, since they are ovoviviparous, some genetic information may be acquired by comparing erythrocyte antigens of females and their pups. Future research in this laboratory will extend the comparative studies already reported, will include quantitative sampling for S antigen frequencies in different geographic areas, and will extend to other elasmobranch species—particularly the larger sharks.

Summary

1. An erythrocyte antigen system of dogfish, *Squalus acanthias,* has been recognized and described with a progression of serological procedures including isoagglutination, antiserum absorption and isoimmunization. This system, the "S" blood group system, contains at least two antigens, "S_1" and "S_2." Individual fish may possess both, either or neither of the antigens, being of blood groups (types) S_1S_2, S_1, S_2 or S_0, respectively. Reagents specific for the antigens have been prepared from normal dogfish sera and absorbed rabbit antiserum, for quantitative studies of blood group frequencies in dogfish from different geographic areas. Fish sampled thus far in the Gulf of Maine (138 individuals) have the following frequencies: S_1S_2—1.4%, S_1—66.7%, S_2—0.7%, and S_0—31.2%. Blood groups of females and unborn pups are compatible with a simple genetic hypothesis of three alleles, S^1, S^2 and S^0, controlling the system.

2. The definitive nature of this system in *Squalus* promises potentially profitable immunogenetic investigations of other elasmobranchs, including the larger shark species. Blood group frequencies can be used in determining the degree of reproductive isolation of populations and may provide information about migrations of fishes.

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An Eastward Extension of the Winter Movement of the Mackerel, *Scomber Scombrus*

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AN EASTWARD EXTENSION OF THE WINTER MOVEMENT OF THE MACKEREL, *SCOMBER SCOMBRUS*.—The capture of one mature and three immature Atlantic mackerel, *Scomber scombrus* Linnaeus, in an otter trawl on March 10, 1960, approximately 180 miles east of Nantucket Island at 41° 24′ N. and 66° 01′ W. in 101 fathoms of water, extends the known eastward, or offshore, winter movement by nearly 100 miles. A bottom temperature of 44.1°F. was recorded by means of a bathythermograph at the end of the half-hour tow. At the same time the surface temperature was 40.9°F.

The mature mackerel measured 41.0 cm. from snout to the fork of the tail; the three immature fish were, unfortunately, lost before they could be closely examined.

The winter range of the Atlantic mackerel as assumed by Sette (1950, *U. S. Fish and Wildl. Serv. Fish. Bull. 51(49):259*), was offshore to about the edge of the Continental Shelf in the deeper water where winter water temperatures are suitable. He had, however, no direct evidence that mackeral were to be found there. His table of winter capture records indicates that no fish had been taken east of 68° 00′ W. longitude in the vicinity of Georges Bank.

Bigelow and Schroeder (1953, *U. S. Fish and Wildl. Fish. Bull. 53(74):320*) state that temperature evidence supports the assumption made by Sette and that mackerel probably winter 30 to 100 miles offshore in water 50 to 100 fathoms in depth and a water temperature of approximately 44° to 46° F.

Fishing effort is at a minimum on the eastern edge of Georges Bank during the winter months, particularly in water deeper than 50–75 fathoms. It is probably for that reason that no records of the offshore limits of the mackerel are available for the colder months.—John B. Skerry, *U. S. Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Massachusetts.*

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EDUCATION AND RECRUITMENT OF OCEANOGRAPHERS IN THE UNITED STATES. *A report by the Committee on Education and Recruitment, American Society of Limnology and Oceanography, Inc., August 30, 1960. Limnology and Oceanography, Supplement to Volume VI. 1960. 23 pp., 2 figs., 4 tables.*

The American Society of Limnology and Oceanography and The Committee on Education and Recruitment deserve credit for recognizing and accepting their responsibility in the education and recruitment of marine scientists. The Committee reports on employment and production of oceanographers, and discusses opportunities and needs in the basic disciplines—biological, chemical, geological, and physical oceanography. The report is well written and organized and contains information of interest to all persons engaged in aquatic sciences. Copies may be obtained from Dr. George H. Lauff, Secretary-Treasurer, American Society of Limnology and Oceanography, University of Michigan, Ann Arbor, Michigan.

The mechanics of such a survey usually present many problems concerning the coverage of institutions for interview and the manipulation of resultant data. That these problems confronted the Committee is evidenced in footnote 3, page viii.

> The statistics reported in this and the following sections of the present report are neither complete nor exact. This is because of the varied nature of the institutions engaged in oceanographic work, the lack of agreement on the definitions of the various categories involved, and the different interpretations which may have been applied to the question by those who answered the questionnaires. . . . Nevertheless, the Committee believes that the numerical information presented supplies a useful indication of the manpower engaged in oceanography . . . .

I hesitate to criticize this report adversely, because (1) it includes much information of value to marine scientists, (2) of my sincere respect for the Committee members who are leaders of note in their respective fields, and (3) as a member of ASLO, I take pride in the Society's publications. To rationalize my position, I consider the subject matter of such import that the limitations and questioned areas of the report cannot be ignored.

The area of disagreement concerns data in Section III—Employment, and the use and conclusions reached from these data in subsequent sections. A major objection is the interpretation of data published in 1959 by the National Academy of Sciences–National Research Council, *Oceanography 1960 to 1970. Chapter 12—Marine Sciences in the United States—1958.* This NAS article listed 70 marine laboratories and summarized results of a survey from 60 of these, but gave no implication that personnel at the 60 institutions represented the total oceanographic working force of scientists in the United States. The ASLO article, on the other hand, accepted NAS figures for the 60 laboratories as the total working force, after apparently deducting approximately 350 visiting scientists from the NAS total of 1,548. ASLO then applied a percentage increase to the NAS figure and concluded that the 24 institutions selected for its survey represented nine-tenths of the present working force. I cannot agree that these institutions include such a high percentage or that they are representative of the distribution of the oceanographic disciplines. Many institutions were not considered, industrial laboratories were not even mentioned, and only two state fishery agencies, Alaska and Virginia, were included in the list. There are more than 20 coastal states, and at least 10 of these maintain a sizable staff of marine scientists. Biological oceanographers (ASLO definition) predominate in these fishery laboratories and, if included in the survey, could substantially change the percentage representation of the several oceanographic disciplines in the total working force. Support of this statement can be found in Carlander's paper, *A Survey of Technical Fishery Personnel* (Transactions of the American Fisheries Society, Volume 88, pages 18–22, January 1959). His 1958 data show over 1,600 technical fishery personnel in the United States, a third of which are in marine fisheries. Using the 15 percent mean annual rate of increase listed by ASLO, the number employed in marine fisheries alone during 1960 would exceed the 629 in the ASLO list in all biological oceanography.

The seriousness of this omission, in terms of percentage representation by discipline, is difficult to determine, but personal knowledge of several industrial laboratories and many of the state agencies omitted leads me to question the ASLO figures. Further, use of these figures to point out that the work force of physical oceanographers is greater than the production does not seem justified. Nor is the following undocumented statement warranted, for it suggests a preconceived notion as to the outcome of the ASLO survey. ". . . The need for strengthening this field [physical oceanography] is confirmed by the fact that there is at present a greater demand for physical oceanographers for employment than for men trained in any of the other specialties."

It would appear from ASLO's own figures (numbers employed and mean annual rate of increase) that the demand for physical oceanographers is no greater than the demand in some of the other disciplines.

During this period of expansion—perhaps the most important to the field of oceanography—a unified front is a necessity, and any discourse favoring a given oceanographic discipline above another will only impede the progress of marine science.

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Factors Related to Commercial Production of the Walleye in Red Lakes, Minnesota

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Factors Related to Commercial Production of the Walleye in Red Lakes, Minnesota[1,2]

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ABSTRACT

Growth of the walleye (*Stizostedion vitreum vitreum*) in Red Lakes, Minnesota, over a 17-year period was slower than in other waters of the Great Lakes region and fluctuated annually from 30.7 percent above to 42.2 percent below mean growth. Individual year classes varied considerably in growth rate. Age distribution in 3½-inch stretch-measure commercial nets varied extremely in 9 years' collections and was related to year-class strength and fishing intensity during periods when classes were available for catch. Abundance of different classes varied 23-fold. Annulus formation and resumption of growth occurred from mid-June to late July. Effective growing season did not exceed 4 months and for some individuals in some years was 2 months or less. The catch contained age-groups II–XII but consisted principally of groups IV–VIII. Seasonal changes in age distribution were dependent on growth rate and fishing effort. Total catch was strongly influenced by growth and seasonal distribution of fishing effort. Maximum availability to commercial nets was at a total length of 15.1 inches, but a large percentage of the catch was smaller fish. Total annual mortality rate after fish attained 15.1 inches total length was 0.66, but continued recruitment through group VIII caused apparent change in mortality rate with increasing age up to IX. Maximum harvest could be attained by concentrating fishing effort in the latter part of the growing season. Abundance indices derived from commercial catch will be strongly influenced by the seasonal pattern of fishing.

INTRODUCTION

A commercial fishery producing up to 1½ million pounds of fish annually is conducted in the Red Lakes of northwestern Minnesota. Of the seven species taken, the walleye (*Stizostedion vitreum vitreum*) provides the greatest poundage and revenue to the fisherman. All fish are caught by Indian residents of the Red Lakes Indian Reservation, within which the lower lake and two-thirds of the upper lake lie. Fish are taken with 3½-inch stretch-measure gill nets and marketed through a cooperative fishery plant. Smith and Krefting (1954) described the general nature of the operation and the production of the fishery over a 25-year period. Their work showed that the wide fluctuation in annual production of walleyes was dependent on strength of individual year classes and that the amount of fishing effort did not appear to influence population size or production in subsequent years. Smith, Krefting, and Butler (1952) demonstrated through marking and recovery studies that walleyes in both the upper and lower lakes belong to the same population. Smith and Pycha (1960) studied the development of Red Lakes walleye during the first year of life. The early life history of the yellow perch (*Perca flavescens*) was studied by Pycha and Smith (1955), and the goldeye (*Hiodon alosoides*) fishery has been described by Grosslein and Smith (1959). The early history of the fishery and preliminary observations of some of the commercial species have been discussed by Van Oosten and Deason (1957).

The Red Lakes have a total area of 275,000 acres and consist of two oval basins connected by a narrow channel (Figure 1). They have a maximum depth of 35 feet and an average depth of approximately 18 feet. Shorelines are sandy and slope gradually into deep water. The lakes are moderately fertile, have a total alkalinity of 120 to 135 p.p.m., and are homothermal. Water temperatures follow air temperatures closely during the summer, and strong currents are created by wind action.

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[2] Publication cost supported in part by the University of Minnesota.

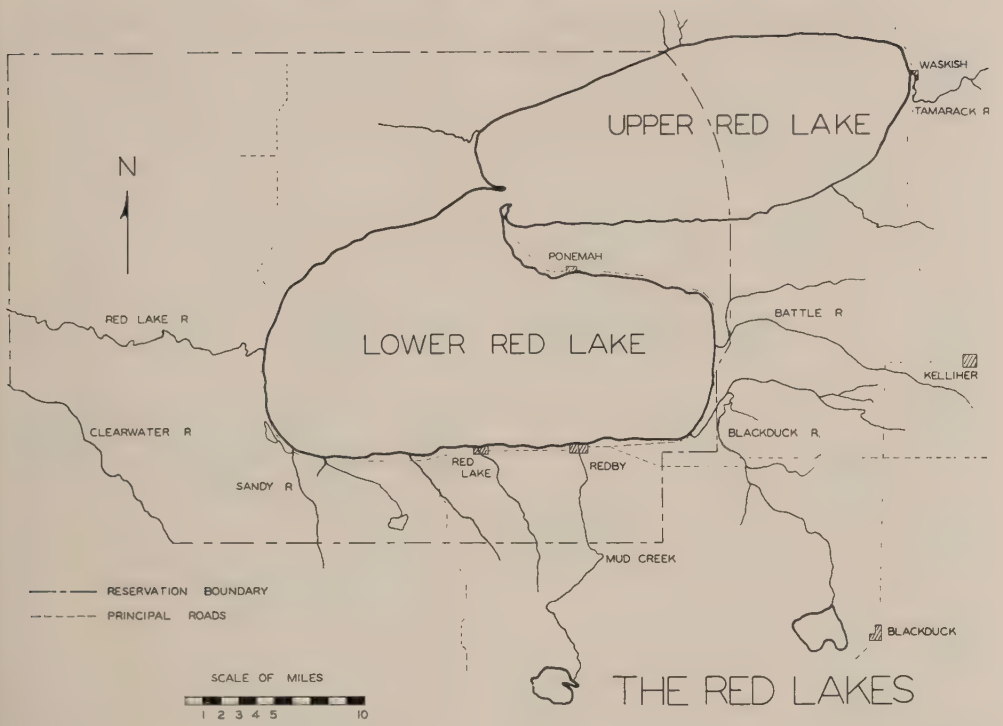

FIGURE 1.—Map of the Red Lakes, Minnesota.

Large areas of submersed weeds are present in the shallow waters, especially on the south and west shores.

The importance of the walleye to the fishery has caused its fluctuations to govern the economic success of the fishing enterprise. For this reason it has been the subject of an intensive investigation over an 11-year period by the senior author. The present study is concerned with a description of the growth characteristics of the walleye, structure of the fishable population, and the factors which influence the contribution of various year classes to the annual walleye production. Since annual production has been shown to be heavily dependent on a few year classes, the problem of prediction of future harvest has been examined and means of obtaining maximum yields from each group have been considered.

The authors are indebted to a number of field and laboratory assistants for their help in collecting and compiling the data presented herein. Robert Butler contributed to the early phases of the work, and Marvin Grosslein, Fred Lux, Robert Knapp, John Magnuson, and Robert Kramer gave substantial aid during the latter period of the study. The U. S. Bureau of Indian Affairs and the management and fishermen of the Red Lakes Fishery Association have cooperated throughout the study, and financial aid has been given by the Ann Arbor Biological Laboratory of the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

MATERIALS AND METHODS

Collection of samples

Samples of fish from which scales and measurements for growth and age-distribution studies were taken have been collected from spawning runs, commercial production as it entered the fishery plant, and from experimental gill-netting. Spawning runs were sampled in 9 years at traps in the Black Duck and Tamarack Rivers and Mud Creek during spawn-taking operations. These samples were separated into males and females and included a total of 35,950 fish. Samples of walleyes were taken in 9 years by experimental gill nets set approximately 1 mile off Redby. These nets consisted of 250-foot gangs of five

alternate meshes ranging in size from 1½- to 4-inch stretch measure. Standard 3½-inch commercial nets 250 feet long were also fished simultaneously. A total of 4,817 fish were secured by experimental fishing.

A third set of samples was taken from the commercial catch. Since the catch for the entire lake is marketed through one fishery, a random selection from this catch was assumed to be a random representation of fish taken by commercial fishermen. In different years the catch was sampled on 12 to 28 separate days during the period from June 15 to August 25. The number of fish sampled in different years ranged from 6,655 in 1950 to 22,273 in 1957, with a total during the period of 113,242 fish. All commerical catches are made in 3½-inch stretch-measure nets and are delivered to the fishery plant in trucks. On sampling days care was taken to select 100-pound boxes of fish representing catches of all general areas in the lake without reference to exact location of catch or name of fisherman.

Age assessment and growth calculation

Growth calculations and age assessments were made from scale impressions on cellulose acetate slides. All scales were read twice, and in difficult groups, three times without reference to previous diagnosis. The age of the fish was determined from the number of annuli present on the scales, or if scale examination indicated that a season's growth had been completed but a new annulus had not yet formed, the total number of annuli present plus one was used as the designation of age. General growth calculations were made from samples of spawning runs and experimental gill nets, because only on these fish was sex determined. Fish of the 1947 year class taken in commercial gill nets were used for special growth analyses. Calculations were made from measurement of projected scale images (x42) recorded on paper tabs and applied to a nomograph designed to incorporate the body-scale relationship in accordance with the method outlined by Carlander and Smith (1944). Age distributions were determined from all commercial samples, selected spawning runs, and experimentally gill-netted fish. The catch statistics used in the calculation of total numbers of fish and total contribution of various year classes to the catch were taken from Smith and Krefting (1954) and from production records of the Red Lakes Fishery Association.

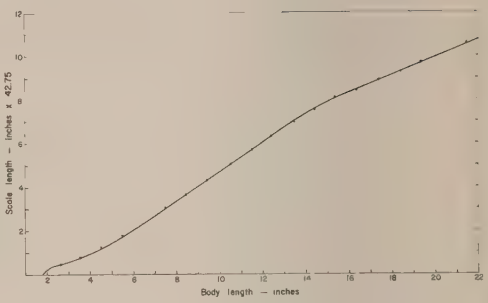

FIGURE 2.—Body-scale relationship of the walleye in Lower Red Lake.

The total length of all fish was measured to the closest 0.1 inch, and weight was recorded to the closest 0.1 ounce. Unless otherwise noted all lengths discussed in the following analyses are total lengths. Year class has been used to designate calendar year of spawning, and age group to designate fish of particular ages without reference to year class.

DESCRIPTION OF GROWTH

Growth of Red Lakes walleyes was determined for 17 year classes collected in 9 calendar years. Of the 5,152 fish used for calculation of growth histories, 3,539 were taken from experimental gill-net samples and the remainder from spawning runs. Nine age groups of fish were covered in the calculations, although some fish of greater age were observed. The old fish were omitted from the general summaries because their individual rates of growth varied greatly and the number was small. Fish from the commercial catch could not be used for growth calculations because the marketing procedure made it impractical to cut the fish to determine sex. Comparison of fish experimentally caught in commercial-type nets with those taken in the commercial catch indicated that fish of similar ages in the two catches had similar lengths at capture. Age distribution in the experimental sets of commercial nets was also comparable to distribution in the commercial catch. It was therefore assumed that the growth rate determined from spawning runs and experimental catches is representative of the growth of fish available to the commercial gear.

Body-scale relationship

Body-scale relationship was determined from 3,041 fish taken from the 1952 and 1955 commercial and experimental catches. Prelimi-

TABLE 1.—*Body length–scale length* (x42) *ratio averaged for the fish in each 1-inch interval*

[Total length in inches of fish is mean for the interval]

Interval	Number of fish	Mean fish length	Mean scale length
2.2–2.9	64	2.60	0.46
3.0–3.9	230	3.52	0.77
4.0–4.9	200	4.51	1.24
5.0–5.9	116	5.46	1.77
6.0–6.9	124	6.42	2.34
7.0–7.9	163	7.46	3.01
8.0–8.9	104	8.42	3.67
9.0–9.9	114	9.43	4.30
10.0–10.9	88	10.50	5.04
11.0–11.9	186	11.48	5.72
12.0–12.9	228	12.40	6.34
13.0–13.9	332	13.47	6.99
14.0–14.9	342	14.41	7.56
15.0–15.9	156	15.32	8.11
16.0–16.9	244	16.32	8.47
17.0–17.9	150	17.39	8.90
18.0–18.9	82	18.42	9.30
19.0–19.9	52	19.35	9.70
20.0–20.9	44	20.37	10.37
21.0–21.9	16	21.46	10.59
22.0–22.9	6	22.03	10.75
Total	3,041	–	–

nary scanning of the data suggested that no simple mathematical function truly represented the average scale length at each body-length interval. To accommodate for changes in the relationship, fish in each 0.1-inch interval from 1.6 inches to 20.5 inches were averaged. A three-point running average of these points was then plotted and a line through these points drawn by eye (Figure 2). Examination of the curve indicates that from a length of approximately 6 inches to 14 inches and from 15.5 inches to 21.0 inches the body-scale relationship is essentially rectilinear, but on different slopes. Below 6 inches the relationship is curvilinear, and scale formation occurs at an average length of 1.6 inches.[3]

Various functions calculated from the data did not represent the empirical relationships throughout the range. No attempt was made to use solutions of any particular function for calculation of length, but lengths at various annuli were determined empirically from the nomograph based on the curve developed in the manner described above. Back calculations by use of this method compared favorably with empirical lengths at time of annulus formation in younger fish. It is believed that this method of growth determination is superior for this population to calculations based on any assumed simple function.

The body length-scale length ratio of fish averaged for each 1-inch interval fell very close to the line projected on the basis of 0.1-inch groups (Table 1).

Average calculated length at each annulus

Upper and Lower Red Lakes.—Since small numbers of fish in the commercial catches come from Upper Red Lake, it was essential to know whether or not the fish from the two lakes grew at different rates. To make this determination, fish from the 1944, 1945, and 1946 year classes collected from the spawning runs in the Tamarack River in the upper lake and the Black Duck River in the lower lake in the spring of 1951 were compared (Table 2). Fish in age-groups V, VI, and VII were selected because any effect of precocious younger fish would thereby be minimized. There were differences presumably caused by sampling for the different groups from the two lakes. Since these differences were not consistent and showed no trend, it was concluded that fish taken in the two spawning runs were representatives of the same population. Tagging studies by Smith *et al.* (1952) confirmed the fact that fish in both lakes were part of the same population. The growth calculations set forth below, however, have been made exclusively on the basis of samples taken from the lower lake.

[3] Fish less than 6 inches total length were taken in seines.

TABLE 2.—*Calculated total length of walleyes at the end of each year of life of the 1944, 1945, and 1946 year classes taken from spawning runs in Upper and Lower Red Lakes in 1951—expressed in inches*

Year class	Lake	Sex	Number of fish	Year of life						
				1	2	3	4	5	6	7
1944	Lower	Male	73	5.3	8.1	10.0	12.2	14.0	15.3	16.0
	Upper	Male	78	5.5	8.3	10.4	12.5	14.2	15.4	16.1
	Lower	Female	98	5.4	7.4	10.0	12.3	14.6	16.4	17.5
	Upper	Female	150	5.6	7.9	10.2	12.4	14.4	15.9	17.2
1945	Lower	Male	66	5.4	8.0	10.7	12.9	14.4	15.2	–
	Upper	Male	89	5.5	8.2	10.8	12.9	14.2	14.9	–
	Lower	Female	31	5.2	8.0	10.9	13.4	15.0	16.3	–
	Upper	Female	78	5.1	8.2	10.9	13.2	14.5	15.8	–
1946	Lower	Male	224	5.6	9.1	11.6	13.1	13.9	–	–
	Upper	Male	219	5.6	9.0	11.4	12.9	13.8	–	–
	Lower	Female	12	5.5	9.1	11.6	13.1	14.8	–	–
	Upper	Female	16	5.8	9.3	12.0	13.8	15.3	–	–

TABLE 3.—*Grand average calculated total length of male walleyes in Lower Red Lake, 1940–1956 year classes—expressed in inches*

Year class	Number of fish	Year of life								
		1	2	3	4	5	6	7	8	9
1940	21	5.3	8.3	9.9	12.1	13.6	14.1	15.1	16.5	17.5
1941	20	5.2	7.4	10.3	12.4	13.3	14.3	15.7	16.8	–
1942	6	4.8	8.1	10.8	12.1	13.5	14.7	15.9	–	–
1943	21	5.0	8.3	9.9	11.9	13.7	15.1	–	–	–
1944	151	5.4	8.2	10.2	12.3	14.1	15.3	16.1	–	–
1945	177	5.4	8.1	10.7	12.9	14.2	14.7	15.5	16.2	16.7
1946	724	5.6	9.0	11.4	12.9	13.5	14.2	14.8	15.1	15.4
1947	500	5.7	8.9	11.0	12.0	13.2	14.0	14.4	14.7	15.5
1948	268	5.9	8.6	10.0	11.9	13.2	13.7	14.3	14.8	15.3
1949	371	5.8	7.8	10.3	12.0	12.9	13.7	14.3	15.0	–
1950	206	5.4	8.3	10.5	11.9	13.1	14.0	14.6	–	–
1951	268	5.6	8.2	9.9	11.7	13.1	14.0	–	–	–
1952	120	6.0	8.3	10.3	12.3	13.6	–	–	–	–
1953	78	5.6	8.6	11.0	12.7	–	–	–	–	–
1954	101	5.9	9.0	11.3	–	–	–	–	–	–
1955	45	6.1	8.8	–	–	–	–	–	–	–
1956	6	5.0[1]	–	–	–	–	–	–	–	–
Total and grand average length	3,083	5.5	8.4	10.5	12.2	13.5	14.3	15.1	15.6	16.1

[1] Calculated from age-group I of the 1957 experimental gill-net catches (1956 year class); all other back calculations made on age-group II or older fish.

Grand average calculated length.—Grand average calculated lengths (Tables 3 and 4) of the walleyes in the 1940-1956 year classes were determined for the first nine seasons of growth. At age IX males and females had an average total length of 16.1 and 17.8 inches, respectively. The divergence in growth rate first appeared at the fifth annulus and became more apparent thereafter. When growth was described on the basis of the sum of mean average increment (Table 5, Figure 3), the divergence of growth between males and females began in the fourth year and was significant by the time the fifth annulus was attained. By the time nine annual increments of growth had been added, the divergence between male and female was slightly less than 2 inches. The percentage annual increment varied from 50.5 percent in the females and 51.2 percent in the males during the second growing season to 6.8 percent in the females and 3.7 percent in the males during the ninth growing season. The rate of increase in the males dropped off sharply during the sixth season and continued to decline, while in the females it progressed steadily through the ninth season.

TABLE 4.—*Grand average calculated total length of female walleyes in Lower Red Lake, 1940–1956 year classes—expressed in inches*

Year class	Number of fish	Year of life								
		1	2	3	4	5	6	7	8	9
1940	20	5.8	8.6	10.2	12.4	14.1	15.0	16.4	18.0	19.5
1941	20	5.4	7.5	10.2	12.3	13.4	14.8	16.7	18.4	–
1942	5	4.4	7.7	10.3	11.7	13.1	14.9	16.9	–	–
1943	22	5.4	8.5	10.2	12.3	14.6	17.1	–	–	–
1944	254	5.5	7.7	10.1	12.4	14.5	16.1	17.0	18.1	18.8
1945	37	5.2	8.0	10.5	12.4	13.7	14.3	15.3	16.4	–
1946	239	5.6	8.9	11.4	12.9	13.7	14.9	15.8	16.3	17.0
1947	224	5.6	8.9	10.9	12.0	13.5	14.7	15.1	15.6	17.1
1948	154	5.9	8.7	10.1	11.9	13.3	14.1	14.8	15.4	16.4
1949	222	5.7	7.8	10.2	12.0	13.0	13.9	14.9	15.8	–
1950	180	5.3	8.3	10.6	12.0	13.2	14.4	15.3	–	–
1951	211	5.5	8.1	9.9	11.6	13.1	14.4	–	–	–
1952	194	6.0	8.1	10.4	12.5	13.9	–	–	–	–
1953	95	5.7	8.8	11.2	13.0	–	–	–	–	–
1954	130	5.8	8.9	11.3	–	–	–	–	–	–
1955	47	6.0	8.7	–	–	–	–	–	–	–
1956	15	5.5[1]	–	–	–	–	–	–	–	–
Total and grand average length	2,069	5.6	8.3	10.5	12.2	13.6	14.9	15.8	16.7	17.8

[1] See footnote 1, Table 3.

TABLE 5.—*Grand average annual increment in length (inches) of male and female walleyes of age-groups I through IX in year classes 1940–1956*

Age group	Male			Female		
	Mean	Sum of means	Percentage increment	Mean	Sum of means	Percentage increment
I	5.50	5.50	–	5.52	5.52	–
II	2.82	8.32	51.27	2.79	8.31	50.54
III	2.18	10.50	26.20	2.20	10.51	26.47
IV	1.76	12.26	16.76	1.78	12.29	16.94
V	1.28	13.54	10.44	1.45	13.74	11.80
VI	0.86	14.40	6.35	1.28	15.02	9.32
VII	0.80	15.20	5.56	1.12	16.14	7.46
VIII	0.72	15.92	4.74	1.00	17.14	6.20
IX	0.60	16.52	3.77	1.18	18.32	6.88

Apparent change in rate of growth

Many studies on various species of fish have noted that fish taken in later years of life appear to have grown more slowly during early years than fish taken during early years of life. In the present study this trend was apparent in Red Lakes walleyes but was not consistent in certain groups. Variations of actual growth rate in the various year classes masked to a considerable extent any tendency for this apparent change in rate of growth to show up in young year classes.

Samples of the 1947 year class were taken in 8 successive years from both commercial and experimental nets. When fish taken from commercial gear were examined for growth rate in each year of collection, it was quite evident that precocious fish were caught early in life and that in later years of collection slower growing fish were taken (Table 6). Variations in calculated length at annulus II were as great as 0.8 inch between fish taken in the third year of life and those taken during the tenth season of growth. Calculated length at annulus III showed a difference as great as 1.0 inch between fish collected at 3 and 8 years of age. The change was progressive in each succeeding year of collection. It was also noted that slower growing fish were caught more frequently as each season progressed. In each year of collection except the last, the calculated length at each annulus was lower for fish taken in August collections than in June collections. Calculations made from August collections in one year were approximately the same or slightly higher than those made from June collections in the following year. These data strongly suggest that the observed changes are caused by the taking of precocious fish in early years and a continued taking of the faster growing fish in each succeeding year in the commercial gear. The change within the season is ascribed to the

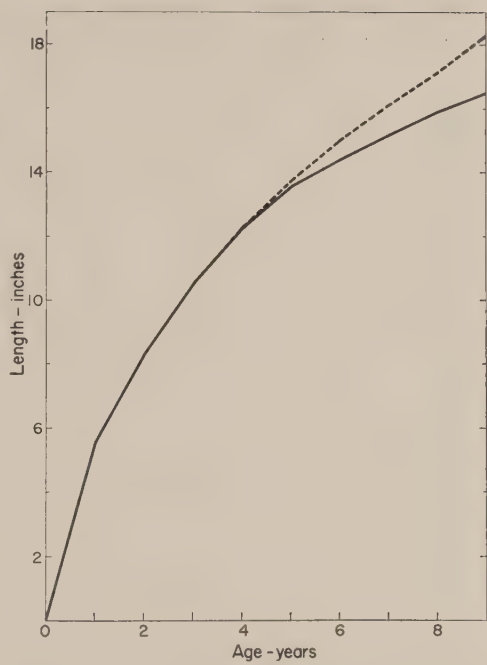

FIGURE 3.—Growth of male and female walleyes expressed as summation of grand average calculated increment in total length. Solid line, males; dashed line, females.

same mechanism. The fact that there is no downward trend between August collections and those of the following June is consistent with this assumption since there is no fishing during the intervening period. A shift in sex ratio, such as is described below, which reduces the relative number of faster growing females after annulus VI does not account for the decline in average growth rate because the trend is marked before this age. Fish of the 1947 year class taken in experimental nets from 1949 through 1955 show similar trends in the case of both males and females. The year classes of 1946, 1948, and 1949 taken in experimental nets also showed similar trends.

The data of Table 6 show a reversal of the downward trend in 1956 especially in calculated growth after annulus IV, and the trend within that season is also reversed. These changes are believed to be caused by a progressive decline in the efficiency of the gear which was noted in the 1956 season. The cotton webbing used in the fishery that year began to deteriorate as early as July 15 and was largely unfishable by the middle of August. The threads stretched easily so that larger fish

TABLE 6.—*Average calculated length in inches of the 1947 year class of walleyes at each annulus in successive months of collection and in different years of collection*

[From unsexed fish taken in commercial gill nets]

Year and month of collection	Number of fish	Age group								
		I	II	III	IV	V	VI	VII	VIII	IX
1949										
July	17	6.4	9.5	–	–	–	–	–	–	–
1950										
June	25	6.1	9.5	11.6	–	–	–	–	–	–
July	22	5.8	9.2	11.3	–	–	–	–	–	–
August	23	5.7	9.1	11.1	–	–	–	–	–	–
1951										
June	36	6.2	9.6	11.7	12.7	–	–	–	–	–
July	33	6.0	9.5	11.5	12.6	–	–	–	–	–
August	30	5.8	9.3	11.3	12.5	–	–	–	–	–
1952										
July	58	5.6	9.1	11.2	12.3	14.0	–	–	–	–
August	48	6.0	9.4	11.3	12.3	13.9	–	–	–	–
1953										
June	53	5.7	9.1	11.2	12.3	13.9	15.3	–	–	–
July	49	5.6	9.0	11.1	12.1	13.7	15.1	–	–	–
August	55	5.4	8.8	10.8	11.9	13.5	14.8	–	–	–
1954										
June	67	5.5	8.9	11.0	12.0	13.6	14.9	15.6	–	–
July	51	5.2	8.7	10.7	11.7	13.3	14.5	15.1	–	–
August	51	5.2	8.7	10.8	11.7	13.3	14.4	15.0	–	–
1955										
June	60	5.3	8.7	10.6	11.7	13.4	14.3	14.9	15.6	–
July	54	5.3	8.7	10.8	11.8	13.3	14.3	14.8	15.4	–
August	51	5.3	8.7	10.8	11.7	13.2	14.2	14.7	15.2	–
1956										
June	62	5.2	8.6	10.7	11.8	13.8	14.7	15.2	16.0	16.8
July	58	5.6	8.9	10.9	11.9	13.5	14.8	15.4	15.9	16.9
August	30	5.6	8.9	11.0	12.1	13.5	14.9	15.8	16.4	17.1

of the age group were more vulnerable to catch than smaller fish. As will be shown subsequently, the rate of catch also fell off instead of rising during the season as is characteristic in the Red Lakes. Since 1956 was a below-average year of growth, these effects were more apparent than would have been the case in a year of rapid growth.

From the observations reported here it appears that in an intensive gill-net fishery the time of sampling during the year and the age at which any year class is taken will influence the estimates of growth to a substantial degree. Unless each year class is sampled in a similar manner, comparisons between classes and averages of growth rate based on summation of growth in several classes will be somewhat in error.

Growth of individual year classes

Growth of individual year classes varied extremely (Tables 3 and 4, Figures 4 and 5). The total growth of fish in a year class after the third season of life appeared to be related to growth conditions during the second and third season. Variations seemed to be greater in the female than in the male. The significance of this difference in growth rate with relation to the fishery is considerable and will be discussed in a later section. The slowest growing year class among those observed was the 1949 group, but it was closely

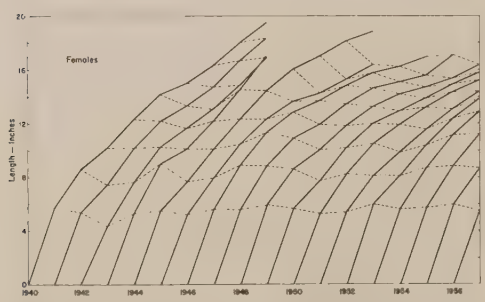

FIGURE 4.—Growth of females of the 1940–1956 year classes of walleyes in Red Lakes.

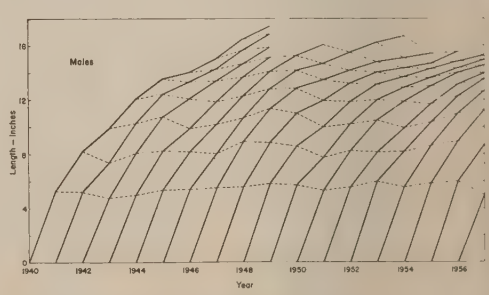

FIGURE 5.—Growth of males of the 1940–1956 year classes of walleyes in Red Lakes.

TABLE 7.—*Percentage of fish of various ages taken in commercial 3½-inch nets with annuli formed at successive weekly intervals in 1951*

[Number, males and females combined, in parentheses]

Week	Age group				
	III	IV	V	VI	VII
June 13–19	–	17 (6)	60 (5)	57 (7)	14 (14)
June 20–26	–	55 (20)	68 (25)	39 (18)	17 (12)
June 27—July 3	100 (2)	60 (5)	0 (3)	14 (7)	0 (2)
July 4–10	–	100 (3)	100 (6)	100 (5)	0 (2)
July 11–17	100 (11)	100 (11)	100 (3)	73 (11)	67 (12)
July 18–24	100 (2)	94 (17)	100 (22)	100 (9)	62 (13)
July 25–31	–	100 (1)	100 (4)	100 (4)	100 (4)
August 1–14	100 (15)	100 (16)	100 (15)	100 (15)	100 (17)

TABLE 8.—*Percentage of fish of various ages taken in commercial 3½-inch nets with annuli formed at successive weekly intervals in 1953*

[Number, males and females combined, in parentheses]

Week	Age group					
	IV	V	VI	VII	VIII	IX and over
July 4–10	–	0 (2)	22 (18)	0 (7)	0 (1)	–
July 11–17	–	80 (5)	42 (45)	24 (29)	–	100 (2)
July 18–24	–	67 (12)	52 (64)	39 (41)	25 (4)	25 (4)
July 25–31	100 (1)	75 (8)	52 (42)	37 (19)	–	40 (5)
August 1–7	–	100 (12)	67 (36)	50 (26)	100 (1)	–
August 8–14	–	–	–	–	–	–
August 15–21	–	100 (10)	93 (46)	88 (16)	50 (2)	–

followed by the 1951 class. At the end of the fifth year of life fish of the 1949 group were the smallest of the entire period (12.9 and 13.0 inches for males and females, respectively). The fastest growing class, judged by the length attained at the end of the fifth year, was the 1944 year class. It had an average length of 14.5 inches for the females and 14.1 inches for males at the time of annulus formation. At 8 years of age the 1941 class was largest in total length.

Time of annulus formation

Beckman (1943) indicated that the time of annulus formation in most species of fishes living in temperate lakes was early in the spring after water temperatures had risen above 53° F. Since a similar assumption has generally been held in many cases where walleyes have been studied, fishes collected after the middle of June in short-term studies have had age assigned on the basis that the annulus was already formed. Extreme variability in growth rate between individuals and discrepancies in strength-of-year-class estimates based on samples of different years suggest the possibility that late annulus formation might account for difficulty in reading and consequent irregularities in the data. It has been assumed by workers using the scale method that annulus formation in temperate climates follows a cessation of growth, which is usually associated with winter conditions, and subsequent resumption of growth in spring. Changes in growth rate associated with maturation of the sex organs and spawning activity often result in the formation of marks similar to characteristic winter marks and may be confused with them. Midsummer growth stoppage associated with extreme high temperature has also been reported.

In the Red Lakes samples of fish were taken throughout the fishing season in 1951 and 1953 to determine the time of annulus formation (Tables 7 and 8). These years were selected because the former was a year of good growth and the latter a year of poor growth. Time of annulus formation in individuals was related to the age of the fish, with younger fish forming annuli earlier than older fish. In 1951, a year of good growth, all group-III fish had formed annuli by the last week in June. Fish of the IV, V, and VI groups all showed annuli by the end of the first week in July. Age-group VII fish, however, had not all formed annuli until the last week of July. In 1953, a year of extremely poor growth, annuli had not been formed in any year class by the end of June. At the end of the first week in July, 22 percent of age-group VI had formed an annulus. By the end of the first week in August all of age-group V had formed annuli, but by the end of the third week in August fish older than age-group V had still not all formed annuli. Only half of group VIII and 88 percent of group VII had formed annuli by the end of the third week in August. The relatively small numbers of fish checked in the year of slow growth reduced the value of these conclusions somewhat, but they emphasize the extreme variability among individuals and age groups and the generally late formation of the annulus which occurred in this year.

The significance of late annulus formation is primarily related to errors in reading of scales, particularly in the years following a season of extremely poor growth and late annulus formation. In populations where very slow growth may be expected in some years,

TABLE 9.—*Annual growth of 801 walleyes in 1955 expressed as percentage of season's growth completed during successive weeks—July 11 to August 21*

[Fish taken in experimental nets]

Week	Sex	Age group								
		I	II	III	IV	V	VI	VII	VIII	IX
July 11–17	Male	–	32	28	24	10	–	8	27	–
	Female	–	–	12	18	37	25	14	11	–
July 18–24	Male	–	25	36	33	39	20	–	0	–
	Female	–	35	30	18	30	29	22	12	–
July 25–31	Male	–	41	34	37	56	25	0	0	0
	Female	–	49	41	59	28	28	80	9	129
August 8–14	Male	72	61	61	49	61	58	51	29	52
	Female	69	62	64	60	58	66	64	51	131
August 15–21	Male	70	65	66	63	71	63	31	40	52
	Female	77	81	63	67	69	75	78	45	–

the validity of age assessment cannot be assured unless several years' collections representing the same year classes are examined.

The causes for late annulus formation are presumbaly those which determine slow growth for the season as a whole. Limited and nonquantitative observations have suggested that years of late annulus formation are usually years in which early summer feeding has been poor. During these years it has been observed that fish are in poor condition and most of them have empty stomachs until mid-July or later. Years of good growth and early annulus formation are related to an early start of ample feeding. The time of annulus formation does not appear to be related directly to temperature since in the Red Lakes temperatures are well above the presumed threshold for the resumption of growth by mid-June or earlier. In many years when fish have not yet formed an annulus by the middle of July they have been subjected to temperatures higher than 65° F. for more than a month. The ecological and physiological significance of these observations has not been explored but would appear to be a fertile field of investigation.

Growth within the season

The percentage of a season's increment of growth in length which has been attained by any particular calendar date will be related to the time of annulus formation and to general conditions controlling growth rate. A year of good growth and one of poor growth were examined in detail to define the range of growth rate within a season. Growth during the season was determined by weekly intervals during the 1955 and 1956 seasons (Tables 9 and 10). Percentages were calculated from total increment as shown in fish taken in the season following the respective year. In view of the apparent slower growth of fish taken in latter years of life already demonstrated, these percentages are based on a total increment that is too small and therefore the percentages are maximum. In a year of good growth (1955) there was no obvious trend in percentage of annual increment attained by a particular date which could be associated with age of the fish. During a season of poor growth (1956) fish of the older groups tended to complete a greater percentage of growth by August than the younger fish. In a year of moderate or poor growth a greater per-

TABLE 10.—*Annual growth of 479 walleyes in 1956 expressed as percentage of season's growth completed during successive weeks—June 27 to August 21*

[Fish taken in experimental nets]

Week	Sex	Age group								
		I	II	III	IV	V	VI	VII	VIII	IX
June 27—July 3	Male	11	14	27	40	19	39	–	–	–
	Female	–	19	25	27	31	–	–	–	–
July 11–17	Male	43	12	9	42	34	–	43	39	–
	Female	20	–	–	–	42	–	46	–	–
July 18–24	Male	–	41	–	25	52	–	54	36	75
	Female	–	50	41	46	54	75	83	77	91
July 25–31	Male	47	43	61	51	60	66	38	43	31
	Female	48	50	46	59	57	38	63	107	–
August 1–7	Male	57	53	57	43	68	52	46	57	–
	Female	48	61	55	57	70	53	54	–	57
August 15–21	Male	64	75	87	69	78	90	91	120	–
	Female	66	76	70	80	123	107	74	59	–

TABLE 11.—*Percentage deviation of increment in length in various calendar years from mean increment of the period 1941–1956*

Year	Male	Female	Average
1941	+ 6.2	+ 7.0	+ 6.6
1942	−24.5	−25.0	−24.8
1943	+21.9	+22.7	+22.8
1944	+18.6	+20.2	+19.4
1945	−17.2	−22.1	−19.7
1946	+ 5.6	+11.8	+ 8.7
1947	+29.2	+32.2	+30.7
1948	+25.9	+25.1	+25.5
1949	+ 4.2	+ 0.5	+ 2.4
1950	−42.8	−41.5	−42.2
1951	+ 3.8	+ 2.9	+ 3.4
1952	− 3.7	0.0	− 1.8
1953	−30.1	−33.8	−31.9
1954	− 3.0	− 6.0	− 4.5
1955	+ 8.4	+ 6.5	+ 7.5
1956	− 2.5	− 0.3	− 1.4

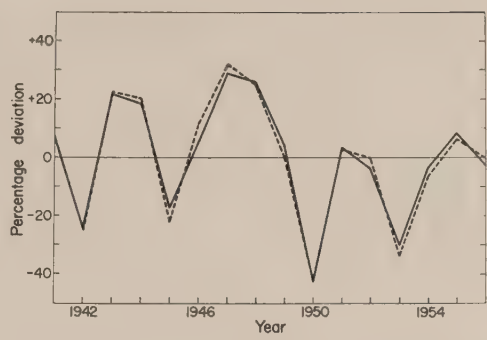

FIGURE 6.—Percentage deviation in separate calendar years from mean annual increment—1941–1956 period. Solid line, males; dashed line, females.

centage of the annual increment was attained by the end of the first week in August than in years of good growth. In a year of poor growth up to 66 percent of the season's total was attained by August 1. In a year of good average growth a smaller percentage had generally been attained by that date. Among fish which were partially or wholly available to the fishery (age-group V and older) 50 percent or more of the season's growth had been attained by August 1. A comparison of the two sexes in different years did not show any clear-cut difference between them. Females had a tendency to put on more of the season's growth early in the summer but individual groups varied greatly. Growth of different year classes during the same season varied considerably but was not consistently related to general growth history of the class.

Variations of growth in different calendar years

Growth and total increment in all age groups of walleyes varied markedly from year to year and influenced the production of the fishery. During years of poor growth fish already available to the commercial gear provided a smaller average contribution for the total number of individuals taken than was the case in a year of good growth. A more important influence on production is that a smaller proportion of fish about to enter the commercial catch do so in years of poor growth because the fishing season is short and coincides with the season of growth. In age groups or sizes which must live an extra year before they are caught because slow growth keeps them from entering the fishery, natural mortality exacts a loss which may be out of proportion to the increased size of the remaining individuals. In order to determine the extent to which slow growth may influence availability of fish, investigation of variation in average growth rate in different calendar years has been made on the basis of percentage deviation from mean increment of all years considered in the manner outlined by Hile (1941). Increments during each calendar year of all age groups except age-group I were used in the compilation, since Smith and Pycha (1960) showed that increments during the first season of life are not closely correlated with those made by older fish.

Estimates of the percentage deviation from the mean annual increment of the period 1941–1956 were made for each sex (Table 11, Figure 6). During this period the minimum increment was 42.8 and 41.5 percent below the mean in 1950 for males and females, respectively. The year of maximum average increment was 1947, when males were 29.2 and females were 32.2 percent above the mean. There was good agreement between males and females in the different calendar years except that females tended to deviate somewhat more in years of much better or poorer than average growth. When the collections for separate years were calculated independently on the basis of combined sexes (Table 12) there was essentially good agreement on the trend in growth rate for the separate calendar years. Discrepancies are presumed to be due to sampling error. The apparent discrepancy for 1947 in the fish collected during 1953 is attributed to a small sample of fish representing growth in that year. The relatively close agreement between the estimate of growth rate in different calendar years made from the individual collections of succeeding cal-

TABLE 12.—*Percentage deviation from mean annual increment in length of walleyes in various calendar years*

[Each year of collection calculated separately and males and females averaged]

Calendar year	Year of collection							
	1950	1951	1952	1953	1954	1955	1956	1957
1944	+12.3	–	–	–	–	–	–	–
1945	–18.3	–	–	–	–	–	–	–
1946	– 9.6	– 2.3	– 3.3	–	–	–	–	–
1947	+21.4	+16.2	+15.8	– 7.1	+16.1	+14.4	–	–
1948	+15.2	+18.4	+16.8	+14.2	+ 9.7	+14.6	+10.1	–
1949	–14.8	+ 1.8	– 2.8	– 2.7	– 0.9	– 6.5	–17.9	–
1950	–	–34.1	–37.9	–34.1	–31.4	–38.0	–45.6	–22.2
1951	–	–	+11.5	+19.0	+19.5	+19.9	+20.5	+14.2
1952	–	–	–	+10.7	+ 8.6	+11.3	+11.9	+ 0.1
1953	–	–	–	–	–21.6	–17.6	– 8.3	–22.3
1954	–	–	–	–	–	+ 1.8	+ 6.7	+ 7.9
1955	–	–	–	–	–	–	+23.0	+11.8
1956	–	–	–	–	–	–	–	+10.8

endar years is strong evidence of the consistency and accuracy of age assessment.

Different age groups responded differently to the factors influencing growth rates in different calendar years. In general the younger groups showed less response to adverse factors than the older groups although the trends were usually in the same direction. Fish of age-group IV and older showed a greater percentage decline in increment during poor years than those of age-groups II and III. Although the deviation from the mean annual increment of the period 1941–1956 fluctuates rather widely, there has been a downward trend through these years. Increment during 1943, 1944, 1946, 1947, and 1948 was greater than during any subsequent year. The lows of 1950 and 1953 were both below those of 1940 and 1945. This trend toward slower growth in each year is also reflected in the slower growth of year classes after 1945. Although the data of Van Oosten and Deason (1957) covering the growing seasons of 1933–1938 are not comprehensive enough to permit calculation of relative growth in different seasons during this period, there was substantially greater total growth of the individual year classes represented in their data than in those year classes treated in the present study. This difference suggests that during the 1930's average growth rates were higher than during the 1950's. Causes for this downward trend are not readily discernible but examination of broad weather trends shows that during the 1930's growing seasons on the average were longer and that total degree days were greater than in the late 1940's and 1950's. During the early 1950's populations of perch were much greater than in most previous seasons and abundance of goldeye, a suitable forage species, declined. While the relationship of these factors to the observed changes in growth rate cannot be defined by available data or their direct influence estimated, trends during the course of the present study and comparison with work done previously on Red Lakes indicate clearly that growth varies enough over a span of years to require periodic adjustment of procedures governing exploitation on the basis of new data. These adjustments would be most necessary in regulations relating to length at capture. Hile (1954) observed a similar long-range trend in growth of walleye in Saginaw Bay and noted that it was greater during the 1930's than before 1929.

Reliability of age determination

Determination of age from scales of the Red Lakes walleye was accomplished by use of the usual criteria applied to ctenoid scales. In general, cutting over of circuli in the lateral fields was the best means of location of the annulus. In years of very poor growth, however, the annulus was not necessarily complete and in older fish confusion of other irregularities with a true annulus increased the difficulty of reading. The validity of the assignment of year marks was attested by the close similarity of growth pattern of fish collected in different calendar years but assigned to the same year class. Since fish were collected over a 9-year period, it was possible to follow the individual year classes and check their relative abundance in succeeding samples. The variations in abundance between the different year classes were consistent in various collections, as will be shown in a subsequent section. Continuous collection throughout the growing season made it possible to establish the time of annulus formation and to determine the exact age of fish which formed the annulus late or which showed little growth. As pointed out above, the goodness or poorness of growth in different calendar years

TABLE 13.—*Weight of walleyes at successive 1-inch intervals calculated from the length–weight curve*

Length (inches)	Weight (pounds)	Increment (pounds)	Percentage increment
6	0.07	0.03	74.4
7	0.11	0.04	60.0
8	0.16	0.05	50.3
9	0.23	0.07	43.2
10	0.31	0.09	37.9
11	0.42	0.11	33.7
12	0.55	0.13	30.4
13	0.70	0.15	27.7
14	0.87	0.18	25.4
15	1.08	0.20	23.4
16	1.31	0.23	21.8
17	1.58	0.27	20.3
18	1.88	0.30	19.0
19	2.21	0.34	17.9
20	2.59	0.38	16.9
21	3.00	0.42	16.0
22	3.46	0.46	15.2
23	3.96	0.50	14.5
24	4.51	0.55	13.9
25	5.11	0.60	13.3

as calculated from collections of succeeding years, showed that the method of age assignment was reliable.

A further criterion was the occurrence of a very narrow area of growth increment on the scale laid down in the 1950 season. This characteristic was so distinctive on the majority of scales collected during the several ensuing seasons that it formed a landmark by which assignment of annuli could be checked for accuracy.

Length–weight relationship

The length–weight relationship of walleyes was determined from 1,604 fish measured to the closest 0.1 inch and weighed to the closest 0.1 ounce. Data were available from fish 6.4 inches to 22.0 inches in total length measured from the tip of the tail lobes to the tip of the snout. The length–weight relationship was described by the formula

$$W = 0.0002786\, L^{3.04957}$$

where W = weight in pounds and L = length in inches. Weights of fish at 1-inch intervals calculated from this relationship are shown in Table 13. Extrapolation of this curve below 6.4 inches does not give the accurate weights which have been determined from young-of-the-year fish taken in various seasons (Smith and Pycha, 1960). From a length of 6.4 inches to a length of 22.0 inches empirical averages of fish grouped by 1-inch intervals compared favorably with the calculated length up to 17.5 inches. Beyond this length empirical weights are less than would be predicted. The small size of the samples of fish above 18.0 inches accounts in part for this discrepancy.

TABLE 14.—*Growth in weight (pounds) of male and female walleyes in the Red Lakes—expressed as calculated weight at time of annulus formation*

[Weight derived from summed grand average calculated increments in length]

Age group	Male			Female		
	Length	Weight	Percentage increment	Length	Weight	Percentage increment
I	5.50	0.05	–	5.55	0.05	–
II	8.32	0.18	256.0	8.31	0.18	242.3
III	10.50	0.36	103.4	10.51	0.36	103.9
IV	12.26	0.58	60.5	12.29	0.59	62.5
V	13.54	0.79	35.5	13.74	0.82	39.5
VI	14.50	0.95	20.7	15.02	1.08	31.2
VII	15.20	1.12	17.9	16.14	1.34	24.4
VIII	15.92	1.29	15.2	17.14	1.62	20.2
IX	16.52	1.44	11.9	18.32	1.98	22.6

It will be noted from Table 13 that between 13 and 17 inches the rate of increase in weight decreases from 27.7 to 20.3 percent. Since this is the length range of maximum availability to the commercial nets, increases in weight will have considerable significance in appraising the effect of any increased size limit on production.

Condition factor or ponderal index has been widely used to appraise changes in body shape of fish or changes in weight at different seasons or between different waters. Variations in stomach contents, state of the gonads, changes associated with length, and other factors have for the most part made calculation of condition factor undesirable except for special studies where the sources of variation could be controlled or measured. Changes in condition throughout the fishing season in the Red Lakes walleye population were determined in various years from June 15 through August. There was a trend toward a higher index of condition as the season advanced, but the pattern of change varied extremely in different years. Average weight of spawning fish of a specified length was somewhat greater than it was for fish taken during the commercial fishing season.

Growth in weight

Growth in weight of walleyes of both sexes (Table 14, Figure 7) was approximately the same during the first 4 years of life, but thereafter the rate of increase declined in the males. It also decreased in females but more slowly. The percentage increase in weight was from 256 and 242 percent during the second season of growth to 11.9 and 22.6 percent in the ninth season for males and females, respectively. At the time of ninth annulus formation males had an average weight of 1.44 pounds and females a weight of 1.98 pounds.

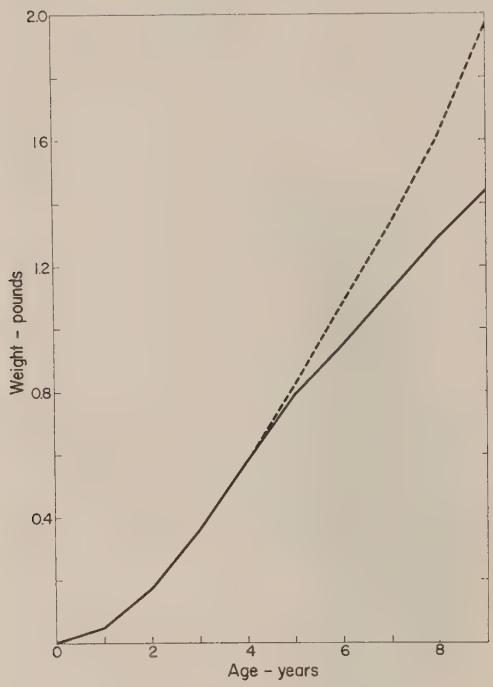

FIGURE 7.—Weight of male (solid line) and female (dashed line) walleyes at time of annulus formation in succeeding age groups—based on calculated weights and lengths.

Growth in weight of various year classes varies with differences in their respective length increments. Difference in males at fifth annulus in different classes may be as great as 0.23 pound and in females 0.28 pound. At ninth annulus the difference may be 0.51 pound for males and 0.98 pound for females.

Comparison with growth in other waters

The growth of walleye pike has been compared with growth in other large waters of the north-central region of the continent (Table 15). Growth during the 1940–1956 period in Red Lakes was slower than in other waters reported by various authors. It is also slower than that reported by Van Oosten and Deason (1957) for Red Lakes during the 1933–1938 period (apparent slower growth during first year is due in part to direct proportion method of calculation). When data from Red Lakes are compared to those from Lake of the Woods, it is apparent that through age-group VI growth was slower during the 1940–1956 period in Red Lakes but roughly comparable during the 1933–1938 period. Since the earlier period in Red Lakes covers a series of years comparable to that reported for Lake of the Woods, it is possible that longe-range fluctuation in the latter lake may show a decline similar to that in Red Lakes. In any case it cannot be assumed on the basis of available data that Red Lakes walleyes grow more slowly than those in Lake of the Woods. Growth reported for Lac la Ronge in Saskatchewan is comparable to early Red Lakes records but faster than growth demonstrated during the present study.

In Lake Erie, Saginaw Bay, and Green Bay growth is much faster than in Red Lakes. This advantage is marked by the end of the

TABLE 15.—*Calculated total length at succeeding annuli of walleyes from various waters—expressed in inches*

Water	Sex	Age group									
		I	II	III	IV	V	VI	VII	VIII	IX	X
Red Lakes	Male	5.5	8.4	10.5	12.2	13.5	14.3	15.1	15.6	16.1	–
	Female	5.6	8.3	10.5	12.2	13.6	14.9	15.8	16.7	17.8	–
Red Lakes[1] (Van Oosten and Deason, 1957)	Male	4.4	8.5	11.4	13.5	14.8	15.9	–	–	–	–
	Female	4.4	8.6	11.6	13.7	15.2	16.7	–	–	–	–
Lake of the Woods[1] (Carlander, 1945)	Male and female	6.4	9.3	11.5	13.5	14.9	16.7	18.2	19.9	21.6	–
Lake Erie[1] (Deason, 1933)	Male and female	6.0	9.7	12.1	15.1	18.0	–	–	–	–	–
Green Bay[2]	Male	7.3	11.4	14.2	16.2	17.9	19.2	20.2	20.8	21.5	22.1
	Female	6.7	10.8	14.2	16.5	18.5	20.2	21.7	23.0	24.2	25.3
Saginaw Bay (Hile, 1954, 1930–1940 group)	Male	6.4	12.0	15.8	18.1	19.5	20.6	21.4	21.9	22.7	–
	Female	6.4	12.0	16.3	18.9	21.3	22.9	24.3	25.4	26.3	–
Lac la Ronge (Rawson, 1957)	Male and female	–	9.2	11.1	12.9	14.9	16.7	18.4	20.0	21.5	–

[1] Adjusted from original data to total length in inches.
[2] Unpublished data compiled by the junior author from fish taken 1949–1957.

TABLE 16.—*Sex ratio of walleyes taken from experimental gill nets in Red Lakes, 1955–1957*

Age group	Number of males	Number of females	Number of males per 100 females
I	87	118	74
II	95	123	77
III	137	145	94
IV	141	123	115
V	142	172	83
VI	138	167	83
VII	87	79	110
VIII	81	54	150
IX	36	18	200
>IX	13	4	325
Total	957	1,003	95

second growing season in both Saginaw Bay and Green Bay. Fish in Saginaw Bay are already more than 40 percent larger at this age than those in Red Lakes, and by the end of the eighth growing season males have a 40 percent and females a 51 percent greater size. The causes of this difference in growth rate may be related to length of growing season or intangible space factors, since the populations of both Saginaw and Green Bays are subject to colder and less fertile water than Red Lakes. The heavy cropping of Red Lakes fish, which takes a high percentage of precocious fish, especially females, reduces the apparent growth rate of older fish. It has been suggested that continued heavy cropping of precocious fish in Red Lakes may have a selective effect that results in a longe-range reduction in growth rate, but available data do not provide evidence of this genetic change.

SEX RATIO

The sex ratio of 1,960 fish of age-groups I–IX taken in experimental gill nets during July and August of 1955, 1956, and 1957 was determined. Fish older than age-group IX were extremely scarce (Table 16), and there was much variation between age groups and in the different years of collection. When all age groups for all years were combined the ratio was 95 males to 100 females. During the first 6 years of life there was a preponderance of females. Age-group IV, in which males predominated, is an exception, but this high calculated abundance of males was caused entirely by the 1955 sample. From age VII through age IX there is an increasing predominance of males until in the ninth and older age groups there are 325 males per 100 females.

In the spawning runs which occurred in the streams tributary to the Red Lakes, males predominated strongly. During some years they were observed to exceed females by 10 to 1 or more. The run of 1949 in the Black Duck River, which was completely checked, had a ratio of 184 males to 100 females. The run of Mud Creek, also completely checked in 1951, had a ratio of 368 males per 100 females. Random samples of other runs made over a 9-year period are not reliable since there is a tendency for the different sexes to be more strongly represented at different periods of the run, but in all cases there was a strong predominance of males.

This predominance of males in stream runs, which has been observed in most other Minnesota runs and which is at variance with the conditions of the Red Lakes population as a whole, is probably the result of several factors. Few females are mature until after the sixth season of growth, whereas the large majority of males are mature after the fifth season. There is also a substantial number of precocious males of age-groups III and IV in the runs. A second important factor is the earlier harvest of females by the fishery. Females are almost completely available to the fishery at some time during their sixth season of growth, while males are not fully available until their seventh season or later. The effect of this differential is demonstrated by the predominance of females through age-group VI and the rapid increase in the proportion of males in the older age groups represented in the catch of experimental nets.

There is some evidence that the females have a greater natural longevity than the males since the few very large and old fish taken are predominantly females.

The conditions in Red Lakes differ from those reported by Carlander (1945) for Lake of the Woods and by Hile (1954) for Saginaw Bay. In both cases a relative increase in the proportion of females with advance in age was noted as early as age-group VI. Hile found that in age-groups VIII–XV only 16.1 percent of all fish were males. These authors attributed the trend to a greater mortality rate among the males.

SIZE AND AGE AT MATURITY

Determination of average age at maturity from fish caught in June, July, and August was difficult because the state of the gonads of fish which will spawn for the first time the following spring often cannot be evaluated with certainty. All estimates of size and age at maturity have therefore been made from spawning runs in streams. This method has serious limitations because precocious young

TABLE 17.—*Length-frequency distribution of male and female walleyes in the spawning runs in streams entering Red Lakes—1949–1958*

Size class (inches)	Male		Female	
	Number	Percentage	Number	Percentage
11.2–11.5	5	<0.1	–	–
11.6–11.9	21	<0.1	–	–
12.0–12.3	165	0.6	–	–
12.4–12.7	503	1.8	2	<0.1
12.8–13.1	1,153	4.2	3	<0.1
13.2–13.5	2,338	8.6	12	0.1
13.6–13.9	3,116	11.6	25	0.3
14.0–14.3	4,150	15.4	116	1.3
14.4–14.7	4,063	15.1	285	3.1
14.8–15.1	3,358	12.5	547	6.0
15.2–15.5	2,720	10.1	833	9.2
15.6–15.9	1,595	5.9	956	10.5
16.0–16.3	1,112	4.1	1,034	11.4
16.4–16.7	755	2.8	958	10.6
16.8–17.1	541	2.0	760	8.4
17.2–17.5	419	1.6	601	6.6
17.6–17.9	281	1.0	478	5.3
18.0–18.3	250	0.9	378	4.1
18.4–18.7	141	0.5	349	3.8
18.8–19.1	103	0.4	350	3.9
19.2–19.5	56	0.2	333	3.7
19.6–19.9	22	<0.1	262	2.9
20.0–20.3	17	<0.1	248	2.7
20.4–20.7	4	<0.1	155	1.7
20.8–21.1	3	<0.1	108	1.2
21.2–21.5	1	<0.1	70	0.7
21.6–21.9	1	<0.1	49	0.5
22.0–22.3	–	–	36	0.4
22.4–22.7	–	–	21	0.2
22.8–23.1	–	–	22	0.2
23.2–23.5	1	<0.1	15	0.2
23.6–23.9	–	–	10	0.1
24.0–24.3	–	–	9	<0.1
24.4–24.7	–	–	7	<0.1
24.8–25.1	–	–	18	0.2
25.2–25.5	–	–	7	<0.1
25.6–25.9	–	–	3	<0.1
26.0+	–	–	6	<0.1
Total	26,894	–	9,066	–

fish enter the run and there is a wide range in strength of year class. The previously mentioned difficulty in securing a random sample from the runs further limits accuracy.

Of 35,960 fish checked during the spawning runs in Tamarack River, Black Duck River, and Mud Creek in the 10-year period 1949–1958, 26,894 were males and 9,066 females (Table 17). Males as small as 11.2 inches were mature and entered the runs in most seasons, but were present in small numbers. During the entire period 15.2 percent of the mature males checked were less than 13.6 inches in length and approximately 65 percent were between 13.6 and 15.5 inches in length. Estimation of age from length measurements on the basis of grand average calculated lengths suggests that a substantial number of age-groups III and IV were in the runs and that a large proportion of all males had completed six seasons of growth or less.

The females were not as closely grouped and were substantially larger than the males. The smallest mature female taken was 12.5 inches long and the largest 26.0 inches. Ten

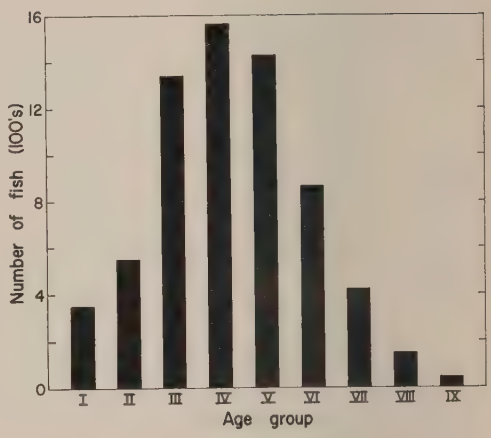

FIGURE 8.—Sum of number of fish per 30 experimental nets each year (1949–1956).

and seven tenths percent of females were 15.1 inches or less in total length and 56.8 percent between 15.2 and 17.2 inches. Approximately 89 percent of the females in the run had completed six or more seasons of growth, and more than 65 percent had completed seven or more.

Selected groups of fish in which age was determined from scales in general support the estimates made above. It would appear that most of the males are mature by the end of the sixth season and most of the females by the end of the seventh season, but that only a small proportion of females spawn until after the sixth season is completed. The wide range in growth rates and strength of year classes makes generalizations concerning age at maturity difficult and of limited applicability to many problems.

AGE DISTRIBUTION

Experimental catches

The age-group distribution of the walleyes in Red Lakes was estimated from experimental and commercial catches. All experimental catches were made in the standard experimental nets, but fishes younger than age-group IV were apparently not caught in proportion to their abundance in the population (Table 18, Figure 8). Although the 1½-inch meshes in the smallest gill net took fish during their second season of growth, the six graded meshes took proportionately less fish of age-groups I, II, and III than were present in the population. This selection, however,

TABLE 18.—*Number and percentage of fish caught per unit of 30 experimental nets each year summed for the period 1949–1957*

[Percentages in parentheses]

Age group	Year									Total
	1949	1950	1951	1952	1953	1954	1955	1956	1957	
I	4 (0.5)	26 (3.3)	18 (2.2)	28 (4.4)	46 (5.3)	11 (1.0)	137 (18.1)	56 (14.1)	19 (3.6)	345
II	102 (12.4)	32 (4.0)	37 (4.6)	50 (7.9)	52 (5.9)	101 (9.3)	30 (3.9)	88 (22.3)	60 (11.3)	552
III	404 (49.1)	253 (31.5)	101 (12.5)	74 (11.7)	85 (9.7)	103 (9.4)	94 (12.4)	46 (11.7)	182 (34.1)	1,342
IV	88 (10.7)	388 (48.2)	398 (49.5)	88 (13.9)	215 (24.6)	163 (14.9)	97 (12.8)	56 (14.1)	73 (13.7)	1,566
V	124 (15.1)	64 (7.9)	239 (29.6)	266 (41.9)	150 (17.1)	321 (29.3)	134 (17.5)	52 (13.3)	77 (14.4)	1,427
VI	64 (7.8)	34 (4.2)	11 (1.4)	120 (18.9)	235 (26.8)	165 (15.1)	150 (19.8)	39 (9.8)	52 (9.8)	870
VII	20 (2.4)	6 (0.7)	1 (0.2)	8 (1.3)	87 (10.0)	182 (16.6)	61 (7.9)	39 (9.8)	22 (4.1)	426
VIII	12 (1.4)	2 (0.2)	–	–	3 (0.3)	43 (3.9)	43 (5.6)	10 (2.4)	36 (6.8)	149
IX and >IX	4 (0.5)	–	–	–	3 (0.3)	2 (0.2)	15 (1.9)	9 (2.2)	12 (2.3)	45
Total	822	805	805	634	876	1,091	761	395	533	6,722

was nearly constant, and strong or weak year classes could be followed from year to year.

In order to equilibrate estimates of age-group distribution in different years, the catch has been reported in terms of take of 30 experimental net sets made in July and August of the various years (Table 18). In two of nine years group-IV fish were taken in greatest numbers, and the largest percentage was represented by age-group IV in 1951 when they comprised 49.5 percent of the entire experimental catch. In 1949 age-group III made up 49.1 percent and in 1952 age-group V, 41.9 percent of the total. After the fifth year of life the percentage of fish in the older age groups fell off rapidly. The largest numbers of age-group VI were taken in 1953 when that group formed 26.8 percent of the catch. In age-group VII the greatest representation was in 1954 when 16.6 percent were of that age. Fish of age-group IX and older comprised in all years less than 2.3 percent of the total catch. The range of numbers in the various age groups in successive years varied up to 6-fold in age-groups IV and V, and over 100-fold in age-group VII. After the fifth year of life the contribution of any particular year class to the population varied extremely. Although these estimates are subject to substantial sampling error, the trends exhibited in year classes are consistent with other information.

Commercial catches

The age composition of the commercial catch in 1949–1957 was determined from 99,544 measured fish and 9,407 fish for which age was determined, or a total of 108,951. After the age of fish from the scale samples had been ascertained, they were grouped in 0.4-inch intervals and the percentage of each group in each interval was applied to the total number of fish measured in this interval to determine the age distribution of the entire sample. The average weight of the fish in each age group was applied to the number of fish in the group in the entire sample to determine the proportion by weight of each age group. The total weight of the sample was then compared to the total weight of the catch and the appropriate factor applied to permit estimation of the total number of fish in each group in the entire commercial catch. By this procedure it was possible to get the total weight and the total number of individuals in each age group in the catch. Since cull fish[4] were sampled separately from the "regulars" and separate weights determined for them, they were treated separately by the same procedure and then added to the totals. The data were grouped by months because it was noted, as will be demonstrated below, that the age composition of the catch varied in the different months. During each month samples were taken at 2- to 5-day intervals to permit assessment of changes in age distribution within the season and to compensate for heavy runs of particular age groups and sizes on particular nights. Observation of variation in runs indicated that a short sampling period in any year would be ineffective for estimation.

In order to make better comparisons be-

[4] Culls are fish less than approximately 12.5 inches, which are graded and weighed separately.

TABLE 19.—*Total production of walleyes and number of summer net-lifts (5-net units) in Red Lakes—1940–1957*

Year	Lifts	Walleye (pounds)	Year	Lifts	Walleye (pounds)
1940	6,614	799,753	1949	9,905	660,124
1941	8,086	929,528	1950	12,768	383,447
1942	12,934	940,887	1951	12,449	556,229
1943	14,816	823,827	1952	7,856	654,210
1944	8,454	969,587	1953	6,883	537,500
1945	10,596	872,694	1954	7,918	634,611
1946	11,092	911,464	1955	9,373	644,454
1947	12,393	977,428	1956	10,835	636,444
1948	10,083	928,512	1957	8,723	666,391

tween years and to correct for differences in total fishing effort, the age distribution was recorded in terms of total number of individuals of each age group caught per 100 net-lifts.[5] Total production and total number of lifts were taken from fishery records (Table 19). On the basis of these values, the average annual catch of each age group was estimated (Table 20).

The commercial catch was primarily dependent on fish in groups V and VI except in some seasons when groups VII and VIII contributed heavily. The extreme variation in contribution of each age group in different years was a function of both the strength and the growth history of different year classes. Slow-growing classes contributed more heavily as age-group VI than as age-group V, while faster growing classes contributed more as age-group V. Age-group V contributed from 12.1 percent (1953) to 64.0 percent in 1951; age-group VI contributed 6.8 percent (1951) to 52.6 percent (1953); and age-group VII from 1.8 percent (1949) to 43.3 percent (1954). Age-group VIII contributed 29.7 percent to the 1955 catch, or approximately twice as much as in the next highest year (1954). On the basis of the 9-year average catch per 100 lifts (Table 21, Figure 9), fish of age-group VI were most prominent (29.8 percent), followed by age-group V (26.4 percent) and age-group VII (19.2 percent). All other age groups combined made up 24.7 percent of the catch.

[5] A lift is five 300-foot nets fished for 1 night.

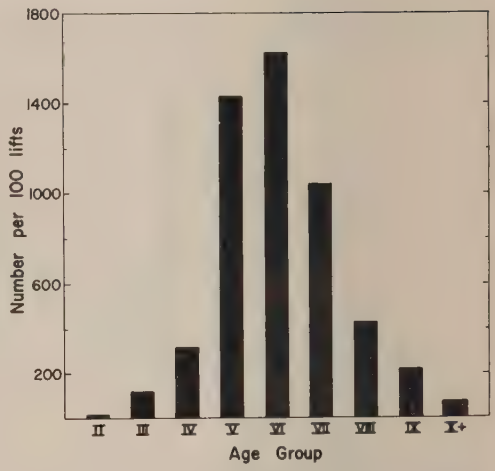

FIGURE 9.—Average number of walleyes in various age groups per 100 5-net lifts per year of commercial 3½-inch gill nets in the Red Lakes—1949–1957.

TABLE 20.—*Number and percentage of each age group of walleyes per 100 net-lifts of commercial 3½-inch gear—Red Lakes, 1949–1957*

[Percentages in parentheses]

Age group	Year of capture								
	1949	1950	1951	1952	1953	1954	1955	1956	1957
II	63 (1.2)	1 (–)	–[1] (–)	5 (0.1)	– –	5 (0.1)	28 (0.5)	9 (0.2)	16 (0.3)
III	348 (6.8)	92 (3.9)	24 (0.6)	70 (0.9)	49 (0.7)	58 (0.8)	99 (1.8)	27 (0.6)	287 (4.7)
IV	342 (8.7)	680 (29.1)	690 (17.5)	289 (3.9)	250 (3.5)	170 (2.3)	195 (3.5)	141 (6.3)	551 (9.1)
V	1,807 (35.2)	326 (13.9)	2,521 (64.0)	3,371 (46.0)	861 (12.1)	1,068 (14.7)	628 (11.4)	683 (15.9)	1,663 (27.4)
VI	1,642 (32.0)	518 (22.1)	269 (6.8)	3,055 (41.7)	3,726 (52.6)	1,559 (21.4)	1,359 (24.6)	1,073 (25.0)	1,364 (22.5)
VII	93 (1.8)	472 (20.2)	173 (4.4)	191 (2.6)	1,992 (28.1)	3,152 (43.3)	1,113 (20.1)	1,123 (26.2)	1,065 (17.6)
VIII	396 (7.7)	70 (3.0)	167 (4.2)	150 (2.0)	83 (1.2)	1,131 (15.5)	1,641 (29.7)	519 (12.1)	677 (11.2)
IX	392 (7.7)	84 (3.6)	39 (1.0)	173 (2.4)	122 (1.7)	87 (1.2)	403 (7.3)	483 (11.2)	222 (3.7)
>IX	46 (0.9)	98 (4.2)	53 (1.4)	31 (0.4)	6 (0.1)	51 (0.7)	64 (1.1)	108 (2.5)	214 (3.5)
Total	5,100	2,340	3,936	7,335	7,089	7,281	5,530	4,166	6,059
Five-net lifts	9,905	12,768	12,449	7,856	6,883	7,918	9,373	10,835	8,427

[1] Less than 0.5 fish.

TABLE 21.—*Number of walleyes caught per 100 5-net lifts of commercial 3½-inch gill nets in the Red Lakes—summation for years 1949–1957*

Age group	Total number (sum)	Average per year	Percentage
II	127	14	0.3
III	1,054	117	2.2
IV	3,308	368	6.8
V	12,928	1,436	26.4
VI	14,565	1,618	29.8
VII	9,374	1,042	19.2
VIII	4,834	537	9.9
IX	2,005	223	4.1
>IX	671	75	1.4
Total	48,866	5,430	–

Change in age distribution during season

The age distribution in the commercial catch varied as the season progressed from June through September in each year. In general there was a shift from older age groups to younger groups as growth brought the latter more completely into the range of the commercial nets (Table 22). The extent of this shift was conditioned by growth during individual seasons, strength of year classes, and to a certain extent by the relative intensity of the fishing load. In all years of the period except 1954, the take of age-group IV increased in relative numbers as the season advanced. This change was as great as from 17.2 to 40.1 percent in 1950, but in other years it was less marked. In 1954, when fishing was carried over into September, the take of age-group IV increased through August and then declined. This change may have been caused by the method of calculation rather than actual conditions. In some years, especially toward the latter part of the period, this trend was also noticeable in the V group. During 1949, when a high proportion of the V group was available to the nets throughout the season, the catch of these fish fell off as the summer progressed. In early years of the sampling period VI-group fish became less numerous in the catch as the season progressed. During

TABLE 22.—*Percentage contribution of various age groups of walleyes to the commercial catch in succeeding months of the 1949–1957 fishing seasons in the Red Lakes*

Year and month	Age group								
	II	III	IV	V	VI	VII	VIII	IX	>IX
1949									
July	1.0	4.9	5.6	37.6	32.4	2.0	7.2	8.5	0.8
August	1.2	6.3	7.0	33.7	33.4	1.8	8.7	6.8	1.1
September	2.2	19.5	10.7	30.3	23.1	1.1	5.8	7.3	–
1950									
June	–	1.7	17.2	9.8	27.7	21.6	9.8	5.4	6.8
July	0.1	1.7	26.9	15.8	23.4	24.2	1.4	2.8	3.8
August	–	8.2	40.1	14.3	16.8	14.1	0.3	3.4	2.8
1951									
June	–	0.1	8.3	51.9	12.4	8.3	9.7	6.0	3.2
July	–	0.6	15.8	62.6	8.4	5.1	5.5	0.4	1.5
August	–	0.8	21.1	68.0	4.2	2.9	1.8	0.4	0.8
1952									
June	–	0.8	3.0	42.6	42.7	2.8	3.8	3.5	0.8
July	0.1	1.0	4.1	42.9	43.8	3.1	1.9	2.6	0.5
August	0.1	1.0	4.2	53.4	37.2	1.6	1.3	1.2	–
1953									
June	–	–	1.2	10.3	47.7	34.6	1.9	4.1	0.1
July	–	0.2	1.9	10.6	55.1	28.2	2.0	1.8	0.2
August	–	1.3	5.5	13.9	53.1	25.3	0.3	0.7	–
1954									
June	0.1	0.6	0.7	4.7	26.1	46.4	18.7	1.6	1.1
July	0.1	1.3	2.6	9.7	16.1	49.7	18.8	1.1	0.7
August	0.1	0.8	2.7	18.5	22.6	39.9	13.6	1.2	0.6
September	–	0.3	2.1	17.3	23.3	41.2	14.0	1.1	0.7
1955									
June	0.3	1.0	2.2	10.1	21.0	22.6	34.5	7.3	1.0
July	0.7	2.4	3.9	9.7	20.5	22.0	29.7	9.9	1.2
August	0.5	1.9	4.1	12.8	27.9	18.0	28.0	5.6	1.2
September	0.2	0.9	2.7	12.7	28.7	18.6	29.1	5.8	1.2
1956									
June	–	0.2	3.4	7.9	28.5	29.6	14.4	13.6	2.5
July	0.2	0.5	4.1	16.0	25.0	27.5	11.8	12.2	2.7
August	0.4	1.1	11.7	22.2	22.1	21.6	10.6	8.0	2.3
1957									
June	–	2.6	5.8	23.0	24.8	16.5	15.8	6.2	5.4
July	0.1	3.0	6.4	22.8	24.7	19.8	14.6	4.4	4.0
August	0.6	7.8	13.9	35.0	19.0	15.6	4.9	1.6	1.6

TABLE 23.—*Average monthly percentage composition of the commercial catch of walleyes in the Red Lakes, 1949–1957*

Age group	Month			
	June	July	August	September
II	0.2	0.3	0.5	1.2
III	1.0	1.7	3.2	6.9
IV	5.2	7.9	12.3	5.2
V	20.0	25.3	30.2	20.1
VI	28.9	27.7	26.3	25.0
VII	22.8	20.2	15.6	20.3
VIII	13.6	10.3	7.7	16.3
IX	6.0	4.9	3.2	4.7
>IX	2.6	1.7	1.2	1.0

the latter part of the period this trend was less marked and in 1953 and 1955 was reversed. Fish 7 years old and older became noticeably less abundant toward the close of the fishing season in all years. In seasons when the most abundant year classes in the fishery had histories of rapid growth, these shifts were most noticeable, especially in age-groups IV and V. Among year classes in which growth was slow throughout life, recruitment continued over a 3-year period and tended to mask the shift.

When the data for all years are combined (Table 23), age-groups III, IV, and V show a progressively increased representation as the season progressed, while group VI showed a slight decline and the VIII and older groups declined sharply. The September estimates are not strictly consistent with the trend noted above because fishing in this month was done in only 3 years of the 9-year period and variations in year-class strength affected the average more than in other months.

Contribution of individual year classes to the fishery

On the basis of the calculations made above it has been possible to estimate the total contribution of various year classes to the fishery between their second and ninth year in both total numbers and total weight (Tables 24 and 25). The maximum yield from any year class observed through its entire period in the fishery was that of the 1947 class which contributed 1,100,000 individuals and 1,228,000 pounds. The minimum contribution was made by the 1945 year class which, exclusive of groups II and III, produced only slightly more than 136,500 individuals and 156,000 pounds. The strongest year classes (1946, 1947) contributed heavily in numbers from the fifth through the seventh year. The 1946 year class made the maximum contribution in any single year when 345,000 pounds of V–annulus fish were produced. The 1947 group, while not contributing as heavily in any single year, continued to produce heavily through the eighth year and as age-group IX made the largest contribution of any year class at that age. In year classes up to and including 1947 the greatest contributions were made by age-groups V or VI. Thereafter, age-groups VI or VII gave maximum yields. It is apparent that a year class may produce its greatest yield at different ages, depending both on its rate of growth and strength of the class. Since the fishery is run on a quota basis the simultaneous presence of two or more strong year classes in the fishery causes their contribution to be stretched out over a greater period. If a single strong year class is in the fishery, its greatest production will occur earlier and will taper off rather rapidly due to the intensity of the fishing pressure which is exerted to fulfill the quota.

Only a small proportion of the total numbers and weights of fish in any year class is produced at ages II and III. The importance of weak year classes in any year's production is evident from a comparison of the contributions of weight by age-groups V and VI. The 1945 class, which was a small contributor, failed to support the fishery during the 1950 and 1951 seasons as other year classes did in following years. Since it had been preceded by a relatively poor class, the 1950 total production was near an all-time low (Table 19). From the foregoing data it is evident that sustained commercial production is dependent on a succession of good year classes, and that the general level of abundance will be strongly influenced by the strength of individual classes.

Estimation of year-class strength

The estimates of the strength of the 1940–1956 year classes were expressed as the sum of the average number of fish per 100 lifts per season of age-groups IV through IX from each year class (Table 26). The average of the estimated sums for all classes was used as a base, and the percentage of this base which each year class represented formed an index of its relative strength. Since all year classes were not represented by complete data for all age groups from IV through IX, various comparisons were made to estimate the sums. Data for the 1945–1948 year classes are complete. The catch per hundred units of group-IV fish from the 1944 year class was back-calculated on the regression from age-group IV to V from the 1945 year class. This pro-

TABLE 24.—*Number of walleyes produced from each year class at different ages—classes 1940–1955*

[Expressed as thousands]

Year class	Age group								Total
	II	III	IV	V	VI	VII	VIII	IX	
1940	–	–	–	–	–	–	–	38.9	–
1941	–	–	–	–	–	–	39.2	10.7	–
1942	–	–	–	–	–	9.2	8.9	4.8	–
1943	–	–	–	–	162.7	60.3	20.7	13.6	–
1944	–	–	–	179.1	66.2	21.6	11.8	8.4	–
1945	–	–	33.9	41.6	33.5	15.0	5.7	6.9	136.6
1946	–	34.5	86.9	313.8	240.0	137.1	89.5	40.7	942.5
1947	6.2	11.7	85.9	264.8	256.5	249.6	168.2	57.2	1,100.1
1948	0.1	3.0	22.7	59.2	123.5	113.5	62.7	19.4	404.1
1949	–[1]	5.5	17.2	84.6	141.5	134.9	59.0	–	442.7
1950	0.4	3.4	13.4	65.0	129.8	92.9	–	–	–
1951	–	4.6	19.4	87.5	119.0	–	–	–	–
1952	0.4	9.5	22.3	145.0	–	–	–	–	–
1953	2.7	3.4	48.1	–	–	–	–	–	–
1954	1.1	25.0	–	–	–	–	–	–	–
1955	1.4	–	–	–	–	–	–	–	–

[1] Less than 100 fish.

cedure was employed because the growth histories of these year classes were similar. The sum for the 1943 year class was estimated by comparison with the sums of groups VI–IX from the 1944 year class. Sums for the 1940–1942 year classes were estimated by comparing age groups with comparable data from the 1946 year class. Growth histories of these year classes were more comparable to that of the 1946 year class than to the 1947 year class. The 1940 and 1941 estimates were adjusted by application of the ratios of the total fishing effort withstood by these year classes to the total effort applied to the 1946 year class. These two classes passed through the fishery during a period of much higher fishing intensity than did the 1946 year class. The catch of group-VIII and IX fish from these classes was presumably much lower than it would have been had fishing intensity been as low as it was while the 1946 year class passed through the fishery. The 1949–1952 year-class sums were estimated by comparison of summations of the catch per 100 lifts of group-IV and older fish to comparable figures from the 1947 year class. Growth histories of these year classes were more similar to the 1947 than to the 1946 year class. Strengths of the 1953–1956 year classes were estimated from the catches per 30 experimental net units by the same procedure as was used for the 1949–1952 year classes. The estimates are most reliable for the 1945–1948 year classes and are less accurate for classes further removed from this period.

Of the 17 classes observed during the present study, that of 1947 was the strongest, but it was closely followed by the 1940 class. The weakest class was that of 1942 which was followed by the 1945 group. Variation in strength between the greatest extremes was 23-fold. There appeared to be little relation-

TABLE 25.—*Poundage of walleyes produced from each year class at different ages—classes 1940–1955*

[Expressed as thousands of pounds]

Year class	Age group								Total
	II	III	IV	V	VI	VII	VIII	IX	
1940	–	–	–	–	–	–	–	72.7	–
1941	–	–	–	–	–	–	68.7	21.2	–
1942	–	–	–	–	–	12.0	4.7	3.7	–
1943	–	–	–	–	229.4	99.0	38.3	23.5	–
1944	–	–	–	211.4	93.4	37.2	17.7	14.9	–
1945	–	–	31.2	44.9	43.2	20.0	7.6	9.5	156.4
1946	–	22.1	82.2	345.3	292.6	165.6	111.5	55.7	1,075.0
1947	2.1	6.2	72.1	274.1	278.4	286.1	210.0	98.9	1,227.9
1948	–[1]	1.5	17.8	56.5	130.3	134.0	93.7	33.5	467.3
1949	–[1]	2.7	11.7	76.3	152.3	184.7	92.0	–	519.7
1950	0.1	1.9	11.1	61.8	162.8	134.6	–	–	–
1951	–	2.4	14.1	98.4	147.0	–	–	–	–
1952	0.1	4.9	33.8	149.2	–	–	–	–	–
1953	1.0	2.4	44.7	–	–	–	–	–	–
1954	0.4	15.8	–	–	–	–	–	–	–
1955	0.5	–	–	–	–	–	–	–	–

[1] Less than 100 pounds.

TABLE 26.—*Estimated strength of 1940–1956 year classes—expressed as percentage of average strength of all classes*

Year class	Number[1]	Percentage of average
1940	11,869	211
1941	3,666	65
1942	560	10
1943	8,182	145
1944	4,666	83
1945	1,298	23
1946	9,782	174
1947	13,063	232
1948	4,563	81
1949	5,112	79
1950	3,506	62
1951	3,761	67
1952	5,803	103
1953	3,126	56
1954	9,801	174
1955	4,579	81
1956	2,397	43
Average	5,631	–

[1] Estimated sum of annual average catch per 100 5-net sets of age-groups IV through IX in each class.

ship between the strength of a year class and the strength of the one immediately following it. Weak classes often preceded strong classes, but the 1947 class, the strongest of the period, was preceded by a strong class.

SELECTIVITY OF NETS

The catch characteristics of commercial 3½-inch nets are an important consideration in Red Lakes because walleyes, yellow perch, and other species must be taken simultaneously. Ideally, a minimum size limit on fish should be set to permit the maximum yield in weight consistent with market needs and the use of efficient gear. Gill nets are sometimes assumed to have rather sharp selection at the lower length limits and to permit minimum size regulation of fish by fixing the mesh size of the net. For spiny-rayed fishes such as the walleye, this lower limit is not well defined. Many fish are tangled in the net or caught by hard body parts at sizes below those which might be expected to be retained in mesh of a particular dimension. The length-frequency distribution of 113,242 walleyes caught in commercial nets was plotted and expressed as numbers per hundred net lifts in each 0.4-inch interval (Table 27, Figure 10). Both limbs of a catch curve representing fish from 8.0 to 23.9 inches are similar. The left limb rises somewhat more abruptly than the right but indicates no sharp selectivity. Fish were most numerous in the 14.8- to 15.1-inch size interval, and a plot by 0.1-inch intervals of this group shows the point of maximum vulnerability to be 15.1 inches total length. It is presumed that an alteration in mesh would displace the curve to the right or left but would not alter its general shape appreciably. When the catch of the nets is viewed on the basis of weight, the peak of the catch curve is at 1.2 pounds.

It is apparent from a comparison of length distributions of the commercial catch and of the spawning runs that fish become less vulnerable after they exceed a particular size since large fish are relatively more plentiful in the spawning run than in the size groups of commercial runs which are presumed to be mature. The effect of this decrease in availability to the 3½-inch nets has not been deter-

TABLE 27.—*Percentage of total catch of walleyes from commercial gear in each 0.4-inch interval and sum of the average annual number per 100 5-net lifts in 1949–1957*

Length (inches)	Number	Percentage	Length (inches)	Number	Percentage
8.0–9.1	13	0.02	15.6–15.9	4,703	9.46
9.2–9.5	16	0.03	16.0–16.3	3,571	7.18
9.6–9.9	40	0.08	16.4–16.7	2,210	4.44
10.0–10.3	40	0.08	16.8–17.1	1,500	3.02
10.4–10.7	100	0.20	17.2–17.5	957	1.92
10.8–11.1	131	0.26	17.6–17.9	594	1.19
11.2–11.5	273	0.52	18.0–18.3	442	0.89
11.6–11.9	362	0.73	18.4–18.7	307	0.62
12.0–12.3	538	1.08	18.8–19.1	241	0.48
12.4–12.7	645	1.29	19.2–19.5	102	0.21
12.8–13.1	880	1.77	19.6–19.9	126	0.25
13.2–13.5	1,483	2.98	20.0–20.3	88	0.18
13.6–13.9	3,073	6.18	20.4–20.7	57	0.11
14.0–14.3	5,568	11.20	20.8–21.1	36	0.07
14.4–14.7	7,275	14.63	21.2–21.5	14	0.03
14.8–15.1	7,763	15.61	21.6–21.9	10	0.02
15.2–15.5	6,561	13.19	22.0–23.9	9	0.02

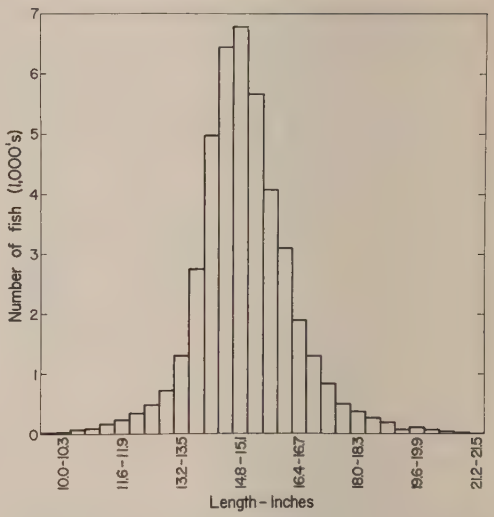

FIGURE 10.—Number of walleyes in each 0.4-inch interval per average 100 5-net lifts of commercial gear—summed for years 1949–1956.

TABLE 28.—*Percentage of each age group and percentage of all walleyes caught in the Red Lakes in commercial (3½-inch) nets below 15.1 inches total length in June, July, and August, 1949–1957*

Age group	Year								
	1949	1950	1951	1952	1953	1954	1955	1956	1957
					June				
II	–	–	–	–	–	100	100	100	–
III	–	100	100	100	–	100	100	100	–
IV	–	90.9	89.5	100	100	100	100	84.3	–
V	–	69.2	74.6	87.4	84.9	87.5	88.9	93.2	–
VI	–	25.0	64.8	57.7	48.0	53.6	67.2	53.4	–
VII	–	12.1	9.0	27.4	28.5	37.3	54.2	45.4	–
VIII	–	0.0	13.1	51.3	18.0	16.8	33.4	24.2	–
IX	–	0.0	0.0	27.1	16.9	0.0	18.8	20.6	–
X and >X	–	0.0	0.0	0.0	–	0.0	0.0	0.0	–
Total catch	–	33.6	56.3	69.3	43.8	40.0	51.7	45.3	–
					July				
II	100	100	–	100	–	100	100	100	–
III	100	100	100	100	100	100	100	100	–
IV	100	94.8	98.8	100	100	100	100	92.2	–
V	57.7	70.2	81.0	84.6	93.9	100	93.6	79.6	–
VI	27.6	29.8	70.1	50.6	58.3	77.8	74.7	58.4	–
VII	19.0	7.4	24.7	28.6	35.7	51.7	47.0	40.0	–
VIII	4.7	0.0	10.9	29.5	9.8	33.3	41.6	30.9	–
IX	1.9	0.0	0.0	21.1	0.0	27.4	27.1	16.5	–
X and >X	0.0	0.0	0.0	0.0	0.0	–	22.7	14.9	–
Total catch	43.0	47.2	74.7	65.6	54.4	58.4	57.1	48.9	–
					August				
II	100	–	100	100	–	100	100	100	100
III	100	100	100	100	100	100	100	100	100
IV	89.4	95.6	94.2	94.7	100	100	96.0	92.1	79.4
V	45.5	68.1	76.6	66.2	83.3	92.9	89.2	69.8	57.8
VI	27.7	33.1	48.5	46.3	57.6	75.4	69.7	46.6	54.1
VII	27.6	22.8	16.6	14.5	36.5	53.1	50.2	38.5	29.8
VIII	0.0	0.0	0.0	40.2	0.0	34.7	43.4	35.6	16.5
IX	0.0	0.0	0.0	22.6	0.0	45.9	20.5	16.9	0.0
X and >X	0.0	0.0	0.0	–	–	0.0	20.6	22.6	0.0
Total catch	38.8	65.1	75.3	58.8	58.1	64.2	59.9	52.1	

mined, but it may result in a higher proportion of very large females in the population than would otherwise occur (Smith *et al.*, 1952).

A large percentage of fish in the commercial catch is below the size of full availability to the nets during the entire fishing season (Table 28). In the various years (1950 to 1956) 33.6 to 69.3 percent were less than 15.1 inches during June. In July, 43.0 to 74.7 percent and in August, 38.8 to 75.7 percent were below the size of full availability.

In no year were any of the fish in age-groups II and III taken at the size of complete availability. In some years none of the age-group IV fish taken were 15.1 inches or above at any time during the season. Not until fish were in age-group VIII were they completely available in any season, and in some seasons some fish of age-groups IX and X were not at the size of complete availability. This slowness of year classes since 1947 to attain size of maximum vulnerability is explained by the decline of growth rates of fish during the period.

As the season progressed no clear-cut trend appeared in the catch of fish below the size of maximum availability. In years of very poor growth the percentage of fish in the older groups below 15.1 inches tended to increase as the season progressed. In years of good growth this trend was less pronounced and was even reversed. The intensity of the fishing in August, the relative strength of year class, and total abundance of fish interacted to produce the variations noted. When fishing intensity is high and fish of fully available size are not abundant, the percentage of small fish is higher.

SEASONAL TRENDS IN CATCH RATE

In 6 of the 9 years sampled the catch per unit of effort of walleyes in terms of number of fish taken (Table 29) was greater at the end of the season than during the first month of fishing. This trend was brought about primarily by the increase in size of individuals during the season which brings a higher percentage of small fish within range of catchability by the nets, and was most pronounced in years when large numbers of young fish were of a size immediately below full avail-

TABLE 29.—*Number of walleyes caught in the Red Lakes per 100 5-net lifts in June, July, August, and September—1949–1957*

Year	Month				Season average
	June	July	August	September	
1949	–	7,021	4,512	2,865	5,100
1950	3,909	2,057	2,124	–	2,341
1951	1,993	4,104	4,828	–	3,936
1952	3,484	8,780	11,922	–	7,335
1953	5,304	6,608	8,711	–	7,089
1954	5,352	5,590	8,434	9,498	7,281
1955	5,130	4,938	5,770	7,205	5,530
1956	5,626	4,933	2,820	–	4,166
1957	5,350	6,320	6,155	–	6,059

TABLE 30.—*Number of 1947 year-class walleyes per 100 5-net lifts during each month of fishing, 1949–1957*

Age group	Year of capture	Month				Season average
		June	July	August	September	
II	1949	–	73	56	63	63
III	1950	65	36	175	–	92
IV	1951	166	650	1,018	–	691
V	1952	1,483	4,546	6,365	–	3,371
VI	1953	2,528	3,639	4,625	–	3,726
VII	1954	2,481	2,778	3,363	4,549	3,152
VIII	1955	1,767	1,463	1,615	2,613	1,704
IX	1956	766	601	249	–	349
X and >X	1957	287	280	97	–	214

ability to the gear. The catches of 1949, 1950, and 1956 did not show this trend although the catch rate was higher in August than in July 1950. In 1949 very few fish were available in the younger groups, especially representatives of the 1945 year class which were entering as fish of age-group IV in August. The extremely poor growing season of 1950 (Table 11) probably accounts for the failure of the catch rate to increase markedly during that season, and the decrease in net efficiency during July and August of 1956, which has been described previously, presumably reduced the normally expected catch in those months. In 1957 growth began unusually early. Of fish taken in experimental gill nets in June, all but one fish of age-groups I to V showed some marginal growth on the scales. By mid-July all fish of age-groups I to IV showed growth increments of 0.5 inch or greater, and all fish of age-group V at least 0.3 inch. The early onset of growth undoubtedly accounts for much of the increase in catch rate from June to July of that year. The slight decline in August cannot be explained on the basis of available data.

The heaviest catches for individual sets are made during the hottest periods of the summer, presumably because change in water temperature and location of food cause maximum fish movement. During these periods more large fish in proportion to the total are taken. Since these catches are sporadic and not consistent, no attempt has been made to analyze them individually and assign definite causes of greater catch.

Causes of changes in catch per unit of effort during the fishing season

If the observed changes in catch per unit of effort from month to month during the fishing season were due entirely to or even principally to changes (increases) in the rate of movement of the fish, a catch curve of an individual year class during the fishing season could show a negative mortality rate. In order to simplify consideration of this problem the 1947 year class alone was followed through its history in the fishery (Table 30).

In 1949 the catch per 100 net units of age-group II was so small that it appeared the catch was entirely accidentals. From 1950 through 1955, the catch per 100 units was higher in the last month of the fishing season than in the first, apparently indicating a negative mortality rate; but in 1956, the apparent mortality rate was again positive. The percentage of each age group caught at a size below full vulnerability to the gear indicates that at all ages from II through IX a sizeable proportion of the 1947 year class was below full vulnerability to the gear (Table 28). It is therefore possible that since the period of fishing covers approximately the period during which growth occurs, the apparent change in availability is a result of increased vulnerability due to growth during the season rather than any marked change in movements of the fish.

In order to check this possibility growth of the commercial fish of the 1947 year class was back-calculated. The number of fish 15.1 inches or greater in length at annulus VI per 100 units of effort was then calculated for June, July, and August of each year from 1953 through 1956 (Table 31, Figure 11). The same calculation for fish 15.1 inches or greater at annulus VII was made for 1954 through 1956 (Table 32, Figure 11). By considering fish greater than 15.1 inches, only fish fully vulnerable to the gear are used, thus eliminating the effect of recruitment on apparent mortality rate. As was expected, except for June and July 1953 the catch per 100 lifts was lower in each successive month during the fishing season. The average total mortality rate of fully available fish appears to be about

TABLE 31.—*Decline in the catch of 1947 year-class walleyes larger than 15.1 inches at annulus VI from 1953 through 1956*

Month and year	Age group	Fish greater than 15.1 inches		Total number of fish caught	Catch per 100 lifts	Number of lifts	Annual survival (percentage)
		Percentage of total	Number per 100 lifts				
1953							
June	VI	61.1	1,450	27,622		1,905.6	
July	VI	49.8	1,698	37,710		2,220.8	
August	VI	31.7	1,453	40,050		2,756.8	
June–August				105,382	1,532	6,883.2	–
1954							
June	VII	31.3	774	7,995		1,033.4	
July	VII	20.5	567	14,820		2,616.0	
August	VII	13.4	449	12,929		2,878.4	
June–August				35,744	549	6,528.0	36
1955							
June	VIII	15.7	277	4,105		1,484.8	
July	VIII	11.3	165	5,773		3,500.8	
August	VIII	6.7	108	3,512		3,248.0	
June–August				13,390	163	8,233.6	34
1956							
June	IX	15.5	118	2,420		2,044.8	
July	IX	25.1	87	3,642		4,187.2	
August	IX	19.6	49	2,246		4,603.2	
June–August				8,308	77	10,835.2	47

65 percent per year. If changes in movements of the fish result in increased availability, these movements do not appear to affect the fully vulnerable segment of the 1947 year class. The increase in catch per 100 units in July over June 1953 may be explained by an unusual circumstance that summer. As has already been shown, almost no growth occurred in June of 1953. The condition of the fish in June was also very poor, and many fish up to 16.0 inches long were culled out of the regular catch because they were so thin. After July 15 the condition of the fish improved rapidly. It is therefore probable that many fish of a length that would ordinarily be fully vulnerable to the gear were only partially vulnerable in June and early July because they were thin. When this condition improved in July, these fish were available to the gear. Since fewer lifts were made in July 1953 than in that month of any other year from 1949 to 1956, it might be anticipated that the catch would be higher per 100 lifts in August 1953 than would otherwise be expected. It will be noted that the catch per 100 lifts did not decline from July to August as much as in most seasons. Most of the growth that did occur in 1953 took place in August. Since the portion of the 1947 year class that is over 15.1 inches does not show increased availability to a perceptible degree as the season progresses, the question as to whether growth of the segment of the population shorter than 15.1 inches can account for the change in catch per unit of effort during the season, remains open. Average lengths of commercial fish at the beginning of the growth season, the growth increment during the commercial season, and

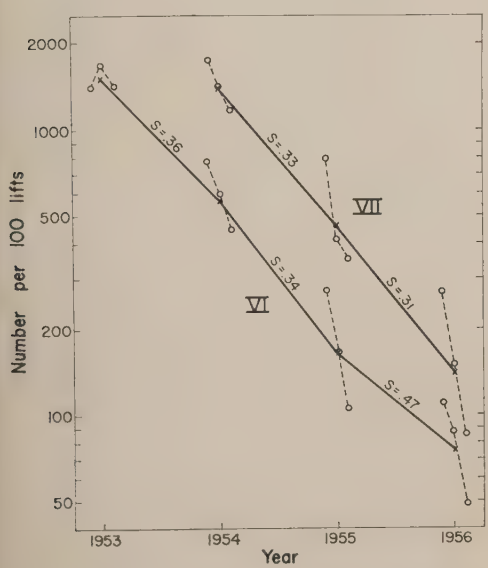

FIGURE 11.—Survival rate of 1947 year-class walleyes calculated for fish 15.1 inches or larger at annulus VI and for those 15.1 inches or larger at annulus VII. Dashed lines represent survival rates from month to month in single seasons.

TABLE 32.—*Decline in the catch of 1947 year-class walleyes larger than 15.1 inches at annulus VII from 1954 through 1956*

Month and year	Age group	Fish greater than 15.1 inches		Total number of fish caught	Catch per 100 lifts	Number of lifts	Annual survival (percentage)
		Percentage of total	Number per 100 lifts				
1954							
June	VII	69.6	1,721	17,791		1,033.6	
July	VII	52.3	1,441	37,708		2,616.0	
August	VII	36.1	1,209	34,792		2,878.4	
June–August				90,291	1,383	6,528.0	–
1955							
June	VIII	46.4	817	12,137		1,484.8	
July	VIII	28.2	410	14,370		3,500.8	
August	VIII	22.3	358	11,616		3,248.0	
June–August				38,123	463	8,233.6	33
1956							
June	IX	35.3	270	5,527		2,044.8	
July	IX	43.0	149	6,231		4,187.2	
August	IX	34.8	86	3,977		4,603.2	
June–August				15,735	145	10,835.2	31

the percentage of the commercial fish less than 15.1 inches long at capture (Table 28), should throw light on the question.

In 1952, 87 percent of the 1947 year-class fish were below 15.1 inches at capture in June. The average increment by August[6] of the 1947 fish was 1.12 inches, which resulted in a decrease in the percentage of fish less than 15.1 inches to 66 percent. When the selectivity of the nets is considered, a rapid rise in the catch per unit of effort during the season is to be expected. In 1953, 1954, and 1955, the percentage of fish less than 15.1 inches increased during the season, and the growth increments were considerably smaller than in 1952. The catch per unit effort might be expected to decline under these conditions, but it did not. Fish of the year class as a whole were larger in the later years, and it is presumed that fish shorter than 15.1 inches were closer to full vulnerability than they were in 1952 and therefore needed less increment in length to reach full availability than they did in 1952. Many fish attained a size just below full vulnerability in 1953. It therefore seems probable that growth of incompletely available fish accounted for the increase in catch per unit in these years.

In all years from 1950 through 1955 the catch per unit is higher in the last month of fishing than in June of the following year (Table 29). This observation would seem to indicate a seasonal change in availability (or high natural mortality), but consideration must be given to two facts before a conclusion is made. The average catch per unit effort in any month should be considered as the catch per unit of effort at the midpoint of effort during the month. In June the first few days of fishing usually result in a high catch per unit effort which then declines rapidly during the remainder of the month. The average for June is therefore considerably lower than the catch per unit at the beginning of fishing. An allowance must also be made for mortality from sources other than regular commercial fishing. During the approximately 9 months of closed season there are several known sources of mortality. First, natural mortality may be substantial, especially during the spawning runs. Second, there is gill-netting by the Indians for home consumption and some unreported commercial sales. Third, there is a significant catch by anglers in Upper Red Lake which is made principally from May 15 to June 15 while the fish are still not well dispersed from the spawning streams. These sources of mortality may account for much of the difference between the late summer catch per unit and the catch per unit in June of the following season. Little mention has been made of condition factor of walleyes, but in all years it is lower in June than in the previous August, a factor which also tends to lower the availability to the nets in June. Consideration of all available data strongly suggests that growth during the fishing season is the principal factor bringing about increased availability as the season progresses.

[6] An increase in size from 13.9 to 15.1 inches would increase the catch per unit slightly more than twofold due to the catch characteristics of the nets.

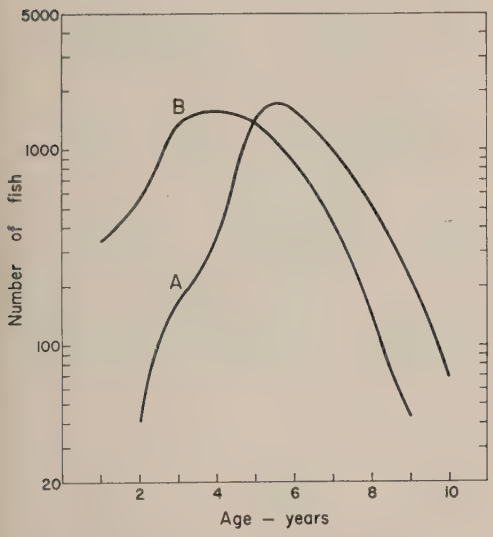

FIGURE 12.—Catch curve of average catch of walleyes (A) in commercial nets, 1939–1955 year classes; and (B) in experimental nets, 1940–1956 year classes. Numbers adjusted to catch per 100 units of commercial gear and equivalent effort with experimental gear.

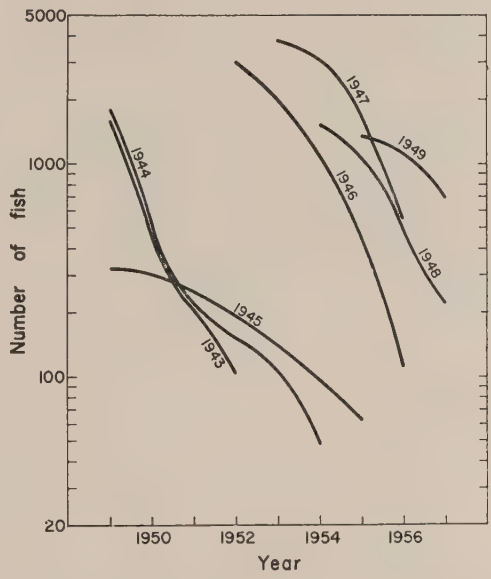

FIGURE 13.—Catch curves of walleyes of individual year classes, 1943 to 1949, in commercial catches of 1949–1957. (Only fish above 15.1 inches included.)

Total mortality of Red Lakes walleyes

To determine the total mortality rate of walleyes a catch curve of the grand average catch per 100 lifts of each age group for the 1949–1957 period was plotted (Table 21, Figure 12A). The right limb of the curve is convex, and apparent mortality ranges from 0.36 between ages VI and VII to 0.66 between ages IX and X. A convex curve indicates decreasing effort through the period, increasing vulnerability of the fish to the gear with increasing age, higher natural mortality with age, or continual but decreasing recruitment over the age range concerned. In view of the continual recruitment, as shown by the 1947 year class, the last factor is known to affect the shape of the curve. The apparent survival of 0.34 between ages IX and X is nearly identical to the rate that applied to the fully vulnerable segment of the 1947 year class (Tables 31 and 32, Figure 11).

Separate catch curves of the 1943–1949 year classes (Table 20, Figure 13) show much variation in both shape and slope and are not entirely consistent with predictions from known growth rates. The 1945 year class grew faster than later classes and was subjected to even higher fishing effort, but its catch curve has less slope. The possibility of either sampling error or mistakes in age determination must be recognized, especially in a weak year class such as 1945. The 1946–1949 year classes all show the effect of recruitment on the curves and all are convex before the eighth year.

A catch curve of the total catch per 30 experimental nets for the 1949–1957 period (Table 18, Figure 12B) is very similar in shape to that derived from the commercial nets of a single mesh size, except that the peak of the curve occurs at age IV instead of age VI and is much more rounded. At corresponding ages the slope of the curve is greater for experimental nets. From age VI to age VII, apparent mortality is 0.51 in contrast to 0.36 from the commercial nets, and from age VIII to age IX it is 0.70 in contrast to 0.66. Experimental nets catch walleyes in the size groups not completely vulnerable to the commercial nets more nearly in proportion to their true abundance in the population than the commercial nets do. This curve must therefore be considered more representative of the true age structure and hence the survival rate than that derived from the commercial net catches.

In this situation the term "mortality rate" is not truly applicable. The catch curve is merely a description of the age structure taken by the nets and may be a rather poor de-

scription of the age structure in the population. It is impossible to evalute exactly the relative strength of any age group below the size of full vulnerability to the commercial gear. The experimental net catch is more representative of the population structure, but the convex catch curve may also be a reflection of continued recruitment even to these smaller mesh nets. The actual average total mortality rate is probably higher than that indicated by the commercial gear and may be higher than that indicated by the experimental gear.

IMPLICATIONS FOR MANAGEMENT

Certain implications about the use of the fishery statistics for management purposes are made apparent by the changes in catch per unit effort during the season, regardless of their cause. The Red Lakes fishery starts operation on about June 15 and continues until a predetermined quota is filled in August or September. In the present analysis, relative abundance has been determined by the season's average catch per unit of effort. The amount of effort, however, in the various months has varied considerably and affects the season's average catch per unit accordingly. In years when considerable fishing is done in June and little in August, such as 1952, the abundance index for the season will be lower than it would have been if the usual fishing pattern had been followed. In years such as 1954 when little fishing is done in June but much in August and September, the abundance index will be higher. The abundance index is therefore an index of the fish available to the nets for a particular seasonal distribution of effort and may be considerably different for a different distribution of effort. A possible refinement might be the use of the average catch per unit effort for some fixed period (such as July 15 to August 15) as a base for an abundance index, but lack of correspondence between "calendar time" and "biological time" in some years might eliminate any advantages over the present index.

Estimates of year-class strength likewise can be made with a reasonable degree of reliability only by considering the catch rate of a year class over a period of several years in order to balance changes in intensity of fishing from month to month and to take account of changes in growth rate. Such an estimate might be in error because there was variation in mortality from causes other than commercial fishing. If non-fishing mortality is substantial, ending a season early will result in the loss of many fully vulnerable fish before the next season's fishing takes advantage of their growth increment.

Prediction of future catches would be desirable in most fisheries. Attempts were made to predict abundance of Red Lakes fish, but were as much as 25 percent in error in some years. At the present time no means of predicting growth is known, and several uncontrollable factors, including market conditions, determine the seasonal pattern of fishing. Fluctuations in growth rate have a considerable effect on the time the fish enter the fishery. Variations in the seasonal pattern of fishing can have a profound effect on the apparent abundance of fish. As an example, in 1952 effort was higher than average in June and lower than average in August. By reversing the amount of effort in the 2 months, it can be calculated roughly that instead of approximately 575,000 fish, 710,000 could have been taken with the same amount of effort, giving an abundance index of about 125.0 instead of 101.5. If no fishing had been done in June, and the additional effort been expended in August, approximately 830,000 fish could have been taken with the same amount of effort, giving an abundance index of about 145. Likewise, the abundance index in 1954 was higher than it was in 1953. It would appear that this was due primarily to the September fishing in 1954, and not due to a greater abundance of fish. Prediction of the next year's catch or, in the case of a quota fishery, the relative abundance, is not possible with enough reliability to be useful under such circumstances, except for extreme fluctuations in abundance.

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hysical Properties of Some Halo-Nitrophenols

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N THE course of a screening program in the search for nemicals selectively toxic to sea lamprey larvae (*1*), it was iscovered that certain mononitrophenols containing halo-ens were effective. The toxic properties of six of these rvicides have been reported (*2*).

The use of these chemicals as larvicides in natural waters equires precise control of concentration. The concentration nust be high enough to be effective against the lamprey arvae, yet not so high as to affect other aquatic species dversely. The concentration of the larvicide can be deter-nined readily by colorimetric analysis.

This article reports certain properties of eight selective arvicides which were measured in connection with the levelopment of colorimetric procedures. Details of the nalysis for one of these, 3-trifluoromethyl-4-nitrophenol, nave been reported (*4*).

EXPERIMENTAL

Compounds Studied. The sources and physical properties of the substituted phenols used are given in Table I.

Ultraviolet and Visible Spectra. The spectrum of each com-pound was determined with a Beckman DU Spectropho-tometer (1-cm. cells) in three solvents: acid, 1% NaOH, and 95% ethanol. Stock solutions of the phenols (usually 500 p.p.m.) were prepared in 1% NaOH and in 95% ethanol. Portions of these were then diluted to suitable concen-trations. To prepare the acidic solutions, the 1% NaOH stock solution was used. The pH of the solution was decreased below 3 by the cautious addition of dilute HCl. In all determinations, the instrument was balanced against the appropriate solvent. The maxima and molar absorp-tivities obtained are reported in Table II.

Each of the phenols shows an absorption maximum in the neighborhood of 400 mμ in 1% NaOH solution. At this value of $\lambda_{max.}$, Beer's law is followed up to a concentration of 30 p.p.m. (Figure 1).

Potentiometric Titrations. The phenol (2 mmoles) was dissolved in water (usually 900 ml.) and titrated with 0.1000*N* NaOH. The pH was measured at intervals with a Beckman Zeromatic pH meter. The pK was calculated at three different points on the titration curve (approximately 40, 50, and 60% neutralization). The average of these three values and the average deviation from the mean are reported in Table III for each phenol.

As the solution became more alkaline, the absorbance in

Table I. Experimental Purification Conditions for Substituted Nitrophenols

Compound	Condition	Recrystallization Solvent	M.P., °C.
	Halo-4-Nitrophenol		
2-Bromo-	Commercial	Benzene–Petroleum ether	110–12
3-Bromo-	Synthesized by authors[a]	[b]	134–35
2-Chloro-	Commercial	Benzene	112–12.5
2,5-Dichloro-	Commercial	Benzene	114.5–16
3-Trifluoromethyl-	Commercial	Benzene–Petroleum ether	75–6
	Halo-2-Nitrophenol		
5-Chloro-	Commercial	Petroleum ether, low b.p.[c]	39.0
3,4,6-Trichloro	Commercial	Petroleum ether	91–2
3-Trifluoromethyl-			71–3

[a] Nitration of *m*-bromophenol in acetic acid (*3*). [b] Crude product m.p. 112°–15° C. was dissolved in acetone and chromatogramed over Al_2O_3. Elution with benzene gave a solution from which the pure compound separated upon addition of petroleum ether. [c] Sample steam distilled before recrystallization.

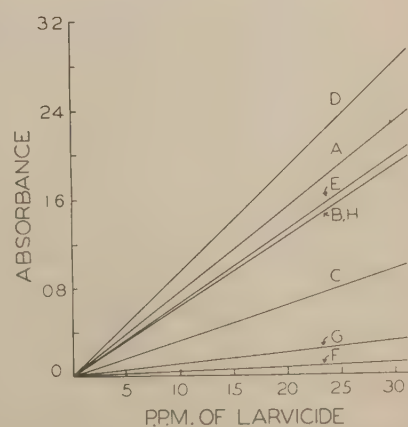

Figure 1. Variation of absorbance with concentration of compounds in 1% NaOH as determined with a Beckman DU Spectrophotometer (1-cm. cell)

A. 2-Bromo-4-nitrophenol (402 mμ)
B. 3-Bromo-4-nitrophenol (397 mμ, indistinguishable from H)
C. 5-Chloro-2-nitrophenol (408 mμ)
D. 2-Chloro-4-nitrophenol (402 mμ)
E. 2,5-Dichloro-4-nitrophenol (393 mμ)
F. 3,4,6-Trichloro-2-nitrophenol (410 mμ)
G. 3-Trifluoromethyl-2-nitrophenol (405 mμ)
H. 3-Trifluoromethyl-4-nitrophenol (395 mμ, indistinguishable from B)

Table II. Absorption Maxima and Molar Absorptivities of Larvicides

Compound	Acid		1% NaOH		95% Ethanol	
	$\lambda_{max.}$, Mμ	$\epsilon \times 10^{-4}$	$\lambda_{max.}$, Mμ	$\epsilon \times 10^{-4}$	$\lambda_{max.}$, Mμ	$\epsilon \times 10^{-4}$
2-Bromo–4-nitrophenol	318	0.78	402	1.69	235	0.81
					317	0.84
					405	0.14
3-Bromo–4-nitrophenol	246	0.484	397	1.37	242	0.74
	312	0.521			305	0.56
5-Chloro–2-nitrophenol	287	0.520	408	0.522	279	0.685
	340	0.311			339	0.390
2-Chloro–4-nitrophenol	316	0.833	402	1.71	315	0.826
2,5-Dichloro–4-nitrophenol	248	0.551	393	1.33	280	0.819
					340	0.480
3,4,6-Trichloro–2-nitrophenol	293	0.209	243	1.05	292	0.461
			310	0.336		
			410	0.0913		
3-Trifluoromethyl–2-nitrophenol	281	0.358	295	0.518	286	0.489
			405	0.234		
3-Trifluoromethyl–4-nitrophenol	280	0.193	300	0.465	290	1.47
			395	1.313		

Table III. Acidity Characteristics of Larvicides

Compound	pK, Average	Minimum pH for Maximum Absorbance
2-Bromo-4-nitrophenol	5.29 ± 0.01	6.5
3-Bromo-4-nitrophenol	6.31 ± 0.01	8.0
5-Chloro-2-nitrophenol	6.43 ± 0.01[a]	8.5
2-Chloro-4-nitrophenol	5.30 ± 0.02	6.0
2,5-Dichloro-4-nitrophenol	4.64 ± 0.01	5.5
3,4,6-Trichloro-2-nitrophenol	3.63 ± 0.04	5.0
3-Trifluoromethyl-2-nitrophenol	5.60 ± 0.00	7.5
3-Trifluoromethyl-4-nitrophenol	6.07 ± 0.03	8.0

[a] Value obtained from titration in 30:70 ethanol:water (v./v.).

determinations, the instrument was calibrated by record the 6.24-micron line of polyethylene film on the pa immediately before the spectrum was run. The princi bands for each of the phenols are given in Table IV.

ACKNOWLEDGMENT

The authors thank Bennett R. Willeford, Buck University, for his help in this study. G.C. Finger, Illi State Geological Survey Division, kindly supplied the trifluoromethyl-2-nitrophenol used.

Table IV. Principal Infrared Bands of Larvicides

Halo-Nitrophenol							
2-Bromo–4-	3-Bromo–4-	5-Chloro–2-	2-Chloro–4-	2,5-Dichloro–4-	3,4,6-Trichloro–2-	3-Trifluoro-methyl–2-	3-Trifluoro-methyl–4-
Microns							
2.95	2.95	3.20	2.90	3.10	3.00	2.90	3.00
6.30	6.20	6.20	6.30	6.40	6.50	6.25	6.00
6.60	6.30	6.35	6.70	6.60	7.20	6.50	6.20
7.60	6.60	6.60	7.50	7.20	7.90	6.75	6.50
8.00	7.55	7.65	8.00	7.40	8.40	7.60	6.70
8.55	7.70	7.90	8.50	7.60	8.60	7.95	6.90
9.00	8.40	8.10	9.00	8.00	8.80	8.50	7.55
9.70	8.95	8.50	9.60	8.25	10.45	8.75	7.85
11.10	9.70	9.15	11.10	8.80	11.10	9.05	8.00
11.25	11.05	9.30	11.20	9.20	11.40	9.40	8.50
12.05	11.50	9.40	12.00	10.35	12.40	10.75	8.75
13.40	12.15	10.90	13.40	11.10	13.45	11.65	9.10
14.50	13.40	11.35	14.00	11.65	14.30	12.45	10.90
	14.70	11.50		11.75		13.20	11.20
		11.85		13.25		13.85	11.35
		12.10		13.60		14.60	11.80
		13.30					11.90
		14.50					13.25
		14.90					13.35
							14.15

the neighborhood of 400 mμ increased because of increasing concentration of phenolate ion. Eventually, a pH was reached above which further increases produced little or no change in absorbance. The absorbance of each phenol was examined as a function of pH using a Bausch and Lomb Spectronic 20 Spectrophotometer. The minimum pH for maximum color development is also reported in Table III. If analysis is to be carried out at these wave lengths, this pH value represents the minimum degree of alkalinity that must be developed in the analytical solution if reliable results are to be obtained.

Infrared Spectra. Infrared spectra were determined on a Perkin Elmer Infracord (NaCl prism) as Nujol mulls. In all

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Fishery Statistical Districts of the Great Lakes

Great Lakes Fishery Commission

TECHNICAL REPORT No. 2
September 1961

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries, between Canada and the United States, ratified on October 11, 1955. It was organized in April, 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: the first, to develop co-ordinated programs of research in the Great Lakes and, on the basis of the findings, recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; the second, to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes. The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties.

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FISHERY STATISTICAL DISTRICTS OF THE GREAT LAKES

By

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United States Bureau of Commercial Fisheries

1961

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FISHERY STATISTICAL DISTRICTS OF THE GREAT LAKES

INTRODUCTION

Biologists responsible for fishery research on the Great Lakes recognized early the futility of attempting to follow changes of fish stocks without full and accurate statistics on catch and effort. The organization of the Great Lakes fisheries, in which landings are distributed among literally hundreds of small ports scattered along thousands of miles of shoreline, makes it impractical to collect the needed statistical records with field agents. The only feasible procedure is a reporting system in which the individual fishermen prepare and submit accounts of their daily take and gear fished.

A start toward the development of a reporting system began in 1926 when John Van Oosten, first Chief of Great Lakes Fishery Investigations, U. S. Bureau of Commercial Fisheries, designed a report form in cooperation with the Michigan Department of Conservation and distributed it for testing among a group of selected fishermen. The trial proved so successful that in September 1927 a form differing little from those now in use throughout the Great Lakes was made official for all commercial fishermen licensed by the State of Michigan. Submittal of reports was initially voluntary, but soon was made mandatory. By 1929 the reporting was sufficiently sound for the records to be used in the catch-effort analyses that have proven so valuable in subsequent years.

The establishment of continuing reporting systems throughout the Great Lakes similar to the one adopted by the State of Michigan was as follows: Ohio, 1931; Wisconsin, 1936; Minnesota, 1944; Ontario, 1948 (experimental use started in 1946); New York, Pennsylvania, Indiana, and Illinois, 1950. For more than 10 years catch-effort statistics have been collected for all Great Lakes fisheries. Procedures for compilation and analysis, developed especially to fit the peculiar conditions of the Great Lakes fisheries, are used by all agencies. The statistical records for the commercial fisheries of the Great Lakes are not uniformly perfect. Changes of fishing gear,

methods, and regulations have made uniform analysis and interpretation difficult. The quality of the statistics is nevertheless high, indeed few of the major commercial fisheries of the world have a better background of statistical information. Trends established from analysis of the more than 30 years of record for the State of Michigan demonstrate the great value of long periods of record and the greater value of each added year.

STATISTICAL DISTRICTS

Inasmuch as fishing conditions are substantially different in various areas of a single lake, the most effective use of catch-effort statistics can be made only if they are sorted according to local areas, or statistical districts. The boundaries of individual districts are fixed after consideration of various factors of which three are especially important. A district should be big enough to yield a sufficiently large catch of the principal commercial species for the catch-effort records to be statistically dependable. A district should be a "natural" division with respect to biological conditions and the nature of fishing operations. District boundaries should be placed so as to minimize difficulties of compilation; if practicable, boundaries should be set between ports—not at ports—and special care should be taken to avoid location of boundaries where most fishermen would regularly operate in 2 or 3 districts. On occasion these criteria may conflict and a compromise must be reached that seems best to fit the local situation.

Experience has sometimes proven that boundaries which appeared sound actually were not practical. The early statistical work on the State of Michigan waters of Lake Michigan, for example, was based on 11 statistical districts. Difficulties in handling the records for the northern part of the lake were so great that after a few years the boundaries were redefined and the number of districts reduced to the present 8. In the Michigan waters of Lake Superior 2 of the original 7 districts were combined because neither of them produced enough fish to provide dependable catch-effort records for important species. More recently the number of statistical districts in the New York waters of Lake Ontario was reduced from 5 to 3 for the same reason.

The boundaries of the statistical districts as presently established appear to be generally satisfactory in both the United States and Canada. Certain weaknesses and imperfections still exist—especially in districts where conditions that dictated placement of the boundaries have changed—but, the weaknesses are insufficient to justify recompilation of large accumulations of reports, and the

harm that would be done to the usefulness of published statistical studies. It cannot be stated categorically that no further changes of boundaries ever will be made—the need for information and the changes in fishery patterns must decide each issue when it arises. It is apparent, however, that revisions of boundaries will be few and not extensive.

A precise definition of statistical districts, supported by maps of individual lakes is especially timely in this period of expanding fishery programs of State, Provincial, and Federal agencies. The need surely will grow for common access to data compiled and analyzed by the different agencies. At this time the catch-effort statistics for all Canadian fisheries of the Great Lakes are treated by the Province of Ontario. The States of Ohio and Minnesota handle their own records. The remaining states (New York, Pennsylvania, Michigan, Indiana, Illinois, and Wisconsin) make preliminary and special tabulations, and the U. S. Bureau of Commercial Fisheries compiles catch-effort statistics for them.

ACKNOWLEDGEMENTS

Many people of the various states and Province of Ontario concerned with the collection, compilation, and analysis of the commercial fishery statistics have provided information on boundaries of statistical districts and have reviewed the compiled descriptions of this report. John Van Oosten of the Bureau of Commercial Fisheries supplied information on the development of the statistical reporting system. Edward Schneberger of the Wisconsin Conservation Department provided information on Wisconsin's boundary with Michigan and Minnesota. Paul Eschmeyer of the Michigan Department of Conservation assisted in obtaining information on the state boundaries of Michigan, and Lee Roach of the Ohio Division of Wildlife assisted in verifying the descriptions of state boundaries of Ohio. Edgar A. Klapp of the International Boundary Commission furnished the latest information on the location of points marking the boundary between Canada and the United States. Illustrations were prepared by William Cristanelli.

DESCRIPTION OF DISTRICTS

The descriptions of boundaries of statistical districts have been based on maps used in tabulating catches (Michigan and Wisconsin), descriptions given in catch summaries (Minnesota and Ohio), or descriptions provided in personal communications (New York and

Ontario). Interstate boundaries are based upon the most recent legal references that could be found. The position of points on the international boundaries are taken from the latest reports and surveys of the International Boundary Commission and rounded to the nearest second of latitude and longitude.

Reference points used in describing interstate and district boundaries are shown on the guide maps accompanying the descriptions of the districts of each lake. Precise location of reference points can be obtained from the "Great Lakes Pilot," Volumes I and II, of Canada (Canadian Hydrographic Service, Ottawa) and the "Great Lakes Pilot" of the United States (U. S. Lake Survey, Detroit), and the accompanying navigation charts published by the two governments. The location of county and township lines, and streams not given in these references can be obtained from official maps of the various states and the Province of Ontario.

Where all waters of a state within a lake are treated as a single district, it is not numbered. When there are more than one, the districts have been numbered following a west-east or north-south sequence for each state or province. Previous publications have frequently used a one- or two-letter prefix to identify districts of states or province within a lake. In this paper a letter prefix designating the state or province is used before every district number. If the state or province has districts in more than one lake, a second letter designating the lake is added to the prefix. Exceptions have been the omission of "O" for Ontario in the districts of the North Channel (NC) and Georgian Bay (GB) of Lake Huron.

Commercial fishing in connecting waters of the Great Lakes is restricted or prohibited. Where such fishing has been done, the catch has been included in the adjoining district unless otherwise indicated in district descriptions.

LAKE ST. CLAIR

Lake St. Clair, although in the Great Lakes chain, is not generally called a "Great Lake." It is, however, an integral part of the lake system and must be included in any compilation of fishery statistics. The commercial catch in the Ontario waters of Lake St. Clair, including the St. Clair and Detroit rivers is combined in a single district (LSC). Commercial fishing is not permitted in the adjacent waters of Michigan.

BOUNDARY LAKES

Commercial catch statistics from the boundary lakes west of Lake Superior are often published with catch statistics of the Great Lakes. The catch from these lakes is summarized by lake separately for both Canada and the United States. These should not be considered as part of Great Lakes fishery statistics.

LAKE SUPERIOR

INTERNATIONAL BOUNDARY

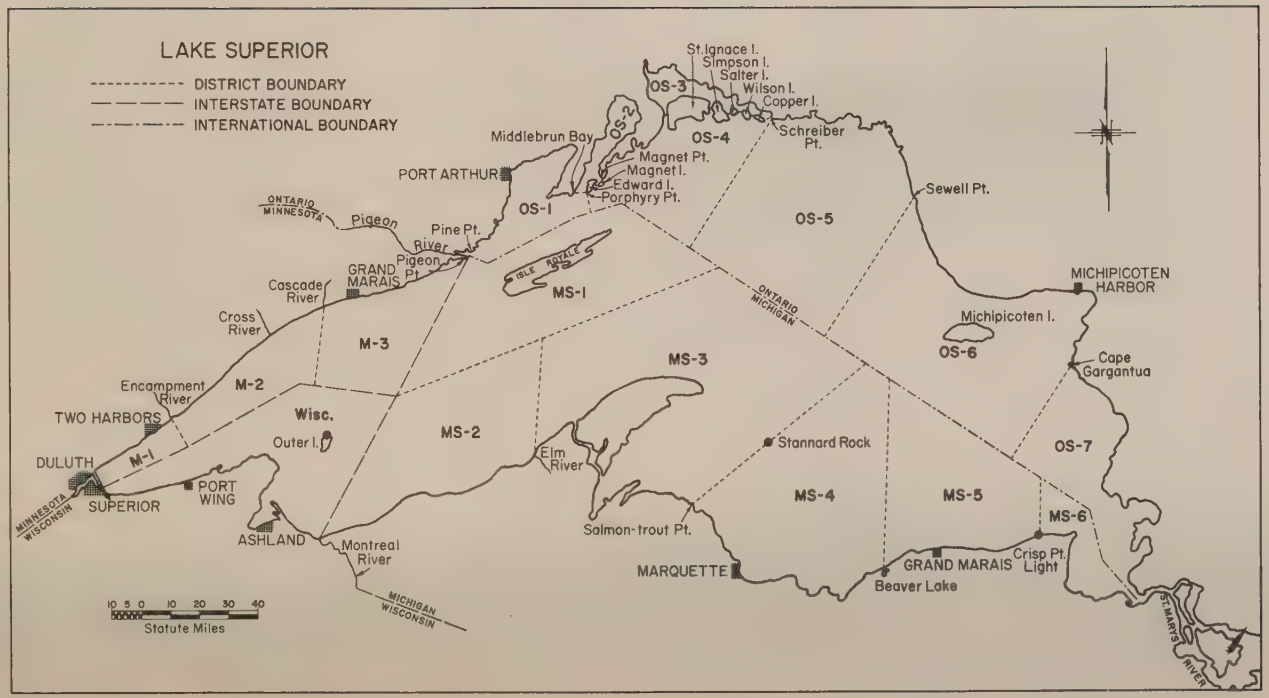
The boundary between Canada and the United States in Lake Superior is a line between the following turning points established by the International Boundary Commission:

Turning point number 261 - latitude 46°27'39", longitude 84°33'25"
Turning point number 262 - latitude 46°38'03", longitude 84°45'46"
Turning point number 263 - latitude 46°53'20", longitude 84°51'37"
Turning point number 264 - latitude 48°18'20", longitude 88°22'07"
Turning point number 265 - latitude 48°14'38", longitude 88°40'45"
Turning point number 266 - latitude 47°58'27", longitude 89°20'14"
Turning point number 267 - latitude 48°00'52", longitude 89°29'21"
Turning point number 268 - latitude 48°00'09", longitude 89°33'53"

INTERSTATE BOUNDARIES

Michigan - Wisconsin and Minnesota

The western boundary of Michigan and the eastern boundaries of Wisconsin and Minnesota in Lake Superior follow a line connecting a point in the middle of the main channel of the Montreal River where it enters Lake Superior (latitude 46°34'05", longitude 90°25'05") and a point where a line drawn through the most easterly point of Pigeon Point and the most southerly point of Pine Point intersects the international boundary (latitude 48°00'50", longitude 89°29'00"),(Mich. Comp. Laws, Sec. 2.202).


LAKE SUPERIOR
DISTRICT BOUNDARY
INTERSTATE BOUNDARY
INTERNATIONAL BOUNDARY
St. Ignace I.
Simpson I.
Salter I.
Wilson I.
Copper I.
OS-3
OS-2
OS-4
Schreiber Pt.
Middlebrun Bay
Magnet Pt.
Magnet I.
Edward I.
Porphyry Pt.
PORT ARTHUR
OS-1
OS-5
Sewell Pt.
ONTARIO
MINNESOTA
Pigeon River
Pine Pt.
Pigeon Pt.
GRAND MARAIS
ISLE ROYALE
MS-1
Cascade River
Cross River
M-3
ONTARIO
MICHIGAN
MICHIPICOTEN HARBOR
Michipicoten I.
OS-6
Cape Gargantua
MS-3
Encampment River
M-2
TWO HARBORS
Wisc.
Outer I.
MS-2
Elm River
Stannard Rock
OS-7
DULUTH
M-1
PORT WING
SUPERIOR
MINNESOTA
WISCONSIN
MS-4
MS-5
MS-6
ASHLAND
Montreal River
Salmon-trout Pt.
MARQUETTE
GRAND MARAIS
Crisp Pt. Light
Beaver Lake
MICHIGAN
WISCONSIN
10 5 0 10 20 30 40
Statute Miles
ST. MARYS RIVER

Wisconsin - Minnesota

The boundary between Wisconsin and Minnesota begins at the midpoint of the boundary between these states and Michigan in Lake Superior (latitude 47°17'30", longitude 87°57'00") and passes through the following points (Minn. Statutes, Chap. 1.15, par. 3):

Latitude 47°18'35", longitude 90°39'15"—a point at the midpoint of a direct line between the mouth of Cross River, Minnesota, and the lighthouse on Outer Island in Wisconsin.

Latitude 46°54'10", longitude 91°31'25"—a point at the midpoint in a direct line between the lighthouse on the shore at Two Harbors, Minnesota, and the light on the lakeward end of the government's east pier at Port Wing, Wisconsin.

Latitude 46°42'39.875", longitude 92°00'24.571"—a point at the midpoint in a direct line, and at right angles to the central axis of the Lake Superior entry between the tops of the eastern ends of the pierheads at the lakeward ends of the Government breakwaters at the Superior entry of the Duluth-Superior harbor.

STATISTICAL DISTRICTS

Michigan

District MS-1 is bounded on the north and east by the International boundary, on the west by the Michigan-Minnesota boundary and on the south by a line on a true azimuth of 64° from the junction of the Michigan-Minnesota-Wisconsin boundaries (latitude 47°17'30", longitude 87°57'00") northeasterly to an intersection with the international boundary.

District MS-2 is bounded on the west by the Michigan-Wisconsin boundary, on the east by a line true north from the mouth of the Elm River to an intersection with the southern boundary of MS-1, and on the north by the southern boundary of MS-1.

District MS-3 is bounded on the west by MS-2, on the north by the southern boundary of MS-1 and the international boundary, and on the east by a line from the northernmost tip of Salmon-Trout Point through Stannard Rock Light to an intersection with the international boundary.

District MS-4 is bounded on the east by MS-3, on the north by the international boundary, and on the west by a line true north from the mouth of the Beaver Lake outlet to an intersection with the international boundary.

District MS-5 is bounded on the west by MS-4, on the north by the international boundary, and on the east by a line true north from Crisp Point Light to an intersection with the international boundary.

District MS-6 is bounded on the west by MS-5, and on the north and east by the international boundary.

Minnesota

District M-1 is bounded on the south by the Minnesota-Wisconsin boundary, and on the east by a line from the mouth of Encampment River to an intercept with the interstate boundary at right angles.

District M-2 is bounded on the west by district M-1, on the south by the Minnesota-Wisconsin boundary, and on the east by a line from the mouth of the Cascade River to an intercept with the interstate boundary at right angles.

District M-3 is bounded on the west by district M-2, on the south by the Minnesota-Wisconsin boundary, on the east by the Michigan-Minnesota boundary, and by the international boundary in Pigeon Bay.

Ontario

District OS-1 is bounded on the south by the international boundary, on the east by a line from Point Porphyry that intersects the international boundary at right angles, and on the north by a line from Middlebrun Island off Middlebrun Bay to Point Porphyry.

District OS-2 is bounded on the south by OS-1 and a line from Pringle Bay on Edward Island to the southwestern point of Magnet Island off Point Magnet, and by the narrow channel between Magnet Island and Point Magnet.

District OS-3 is bounded on the south by a line from Schreiber Point to the eastern point of Copper Island, thence westerly through the midpoints of channels between Copper, Wilson, Salter, Simpson and St. Ignace Islands, and the mainland to the west.

District OS-4 is bounded on the north by districts OS-2 and OS-3, on the west by district OS-1, on the east by a line southwesterly from Schreiber Point to an intercept with the international boundary at right angles, and on the south by the international boundary.

District OS-5 is bounded on the west by OS-4, on the south by the international boundary, and on the east by a line from Sewell Point southwesterly to an intercept with the international boundary at right angles.

District OS-6 is bounded on the west by OS-5, on the south by the international boundary, and on the east by a line from Cape Gargantua southwesterly to an intercept with the international boundary at right angles.

District OS-7 is bounded on the west by OS-6, and on the south and east by the international boundary.

Wisconsin

The Lake Superior waters of Wisconsin comprise a single statistical district.

LAKE MICHIGAN

INTERSTATE BOUNDARIES

Indiana - Illinois and Michigan

The Indiana waters of Lake Michigan are bounded by a true north extension of the Indiana-Illinois border to an intersection with a true east-west line passing through a point 10 miles north of the southern extreme of Lake Michigan which forms the land boundary between Indiana and Michigan (Indiana Constitution, Art. 1, par. 1).

Illinois - Michigan and Wisconsin

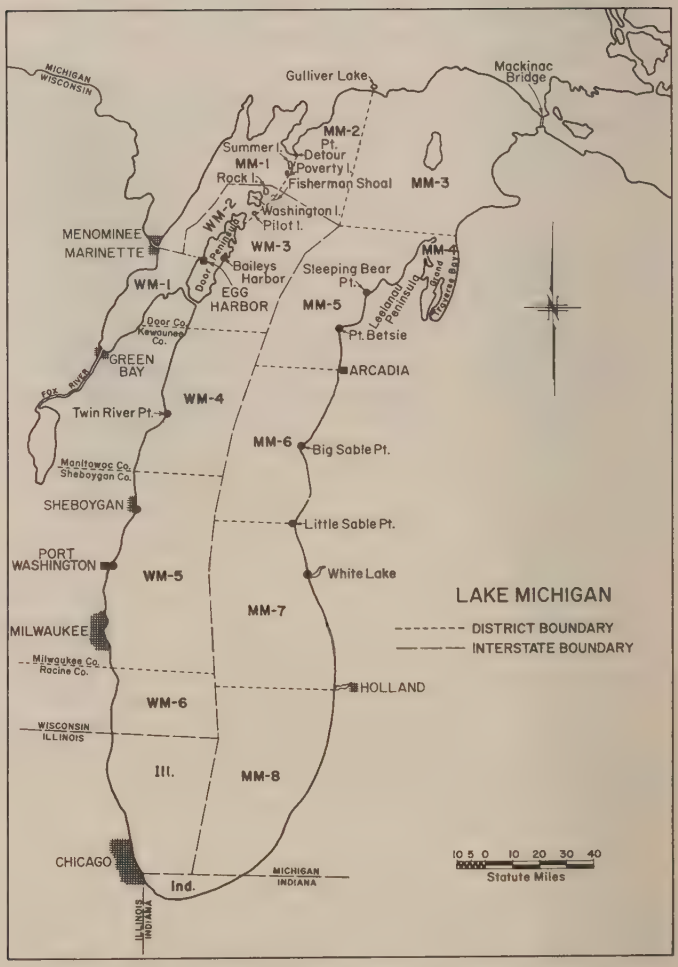
The Illinois waters of Lake Michigan are bounded on the south by the Indiana-Illinois boundary to a point equidistant from each shore on the northern boundary of Indiana, thence north on a common boundary with Michigan to a point equidistant from each shore on latitude 42°29'37" (at longitude 87°01'15", Mich. Comp. Laws, Sec. 2.201) which forms the boundary with Wisconsin to the north (Constitution of Illinois, Art. I). A straight line between the midlake points at the latitudes of the northern boundaries of Indiana and Illinois closely approximates the "middle of the lake" boundary called for in the Illinois Constitution.

Michigan - Wisconsin

The boundary between Michigan and Wisconsin in Lake Michigan starting at the southeastern corner of Wisconsin at latitude 42°29'37", longitude 87°01'15" (a point equidistant from either shore on a line which is the eastward continuation of the boundary line between Wisconsin and Illinois) extends northward through the following points (Mich. Comp. Laws, Sec. 2.201):

Latitude 43°22'50", longitude 87°08'50"—a point equidistant from either shore on a line drawn through the Port Washington fog signal and storm signal, and the White Lake storm signal.

Latitude 43°42'00", longitude 87°07'20"—a point equidistant


MICHIGAN
WISCONSIN
Gulliver Lake
Mackinac Bridge
Summer I.
MM-2
Pt. Detour
MM-1
Poverty I.
Rock I.
Fisherman Shoal
MM-3
WM-2
Washington I.
Pilot I.
MENOMINEE
MARINETTE
WM-3
Door Peninsula
Baileys Harbor
Sleeping Bear Pt.
MM-4
WM-1
EGG HARBOR
MM-5
Leelanau Peninsula
Grand Traverse Bay
Door Co.
Kewaunee Co.
Pt. Betsie
GREEN BAY
ARCADIA
Fox River
WM-4
Twin River Pt.
MM-6
Big Sable Pt.
Manitowoc Co.
Sheboygan Co.
SHEBOYGAN
Little Sable Pt.
PORT WASHINGTON
WM-5
White Lake
LAKE MICHIGAN
MM-7
MILWAUKEE
DISTRICT BOUNDARY
INTERSTATE BOUNDARY
Milwaukee Co.
Racine Co.
HOLLAND
WM-6
WISCONSIN
ILLINOIS
Ill.
MM-8
CHICAGO
10 5 0 10 20 30 40
Statute Miles
MICHIGAN
INDIANA
Ind.
ILLINOIS
INDIANA

from either shore on a line drawn through the Sheboygan storm signal, fog signal, and radio beacon, and Little Sable Point light.

Latitude 44°07'55", longitude 87°00'45"—a point equidistant from either shore on a line drawn through the Twin River Point light and fog signal, and Big Sable light and fog signal.

Latitude 44°52'50", longitude 86°41'10"—a point equidistant from either shore on a line drawn from Bailey's Harbor inland light, and Point Betsie fog signal, radio beacon, and distance finding station.

Latitude 45°05'20", longitude 86°29'30"—a point equidistant from either shore on a line drawn through Pilot Island light and fog signal, and Sleeping Bear Point light.

Latitude 45°14'10", longitude 86°14'55"—a point determined by the United States Supreme Court decree of March 16, 1936, which point is 45,600 meters from the center of Rock Island passage on a true azimuth of 120°.

The boundary between Michigan and Wisconsin in Green Bay (U. S. Supreme Court, 297 US 547, 58 S. Ct. 584) terminating at the last mentioned point above, originates at a point midway between the outer ends of the Menominee Harbor piers, thence on a true course of azimuth 101°15' for 11,470 meters (approximately 7.13 statute miles);

Thence on a true course of azimuth 11°45' for 14,250 meters (approximately 8.85 statute miles);

Thence on a true course of azimuth of 58°50' for 8,290 meters (approximately 5.15 statute miles);

Thence on a true course of azimuth 42°18' for 16,780 meters (approximately 10.43 statute miles);

Thence on a true course of azimuth 28°10' for 11,580 meters (approximately 7.20 statute miles);

Thence on a true course of azimuth 90° for 27,170 meters (approximately 16,88 statute miles);

Thence upon a true course of azimuth 120° for 45,600 meters (approximately 28,33 statute miles).

STATISTICAL DISTRICTS

Illinois

The Lake Michigan waters of Illinois comprise a single statistical district.

Indiana

The Lake Michigan waters of Indiana comprise a single statistical district.

Michigan

District MM-1 is bounded on the southeast and south by the Michigan-Wisconsin boundary in Green Bay, and on the east by a line from the eastern tip of Pt. Detour, to the easternmost edge of Summer Island, thence to an intersection with the Michigan-Wisconsin boundary on a line from the easternmost edge of Summer Island through the navigation light on Fisherman Shoal.

District MM-2 is bounded on the west by MM-1, on the south by the northern boundary of Wisconsin east of MM-1, and on the east by a line from the mouth of Gulliver Lake outlet to the northeast corner of the Michigan-Wisconsin boundary in Lake Michigan (latitude 45°10'14", longitude 86°14'55").

District MM-3 is bounded on the west by MM-2, on the east by Mackinac Bridge, and on the south by a line from the northeast corner of the Michigan-Wisconsin boundary in Lake Michigan across the northernmost tip of Leelanau Peninsula to an intersection with the east shore at the mouth of Grand Traverse Bay.

District MM-4 includes all of Grand Traverse Bay, and is bounded on the north by MM-3.

District MM-5 is bounded on the north by MM-3, on the west by the Michigan-Wisconsin boundary, and on the south by a line true west from the entrance to Arcadia harbor to an intersection with the interstate boundary.

District MM-6 is bounded on the north by MM-5, on the west by the Michigan-Wisconsin boundary, and on the south by a line true west from Little Sable Point to an intersection with the interstate boundary.

District MM-7 is bounded on the north by MM-6, on the west by the Michigan-Wisconsin boundary, and on the south by a line true west from the entrance of Holland harbor at Lake Macatawa to an intersection with the interstate boundary.

District MM-8 is bounded on the north by MM-7, on the west by the Michigan boundary with Wisconsin and Illinois, and on the south by the Michigan-Indiana boundary.

Wisconsin

District WM-1 in southern Green Bay is bounded on the north by the first leg of the Wisconsin-Michigan boundary from the Menominee Harbor Piers (azimuth 101°15') and the easterly extension of this line to the northern tip of the point forming the southwestern side of Egg Harbor, on the Door Peninsula.

District WM-2 is bounded on the south by WM-1, on the west and north by the Wisconsin-Michigan boundary, and on the

east by the portion of a line from the easternmost edge of Summer Island to the navigation light on Fisherman Shoal that is south of its intersection with the interstate boundary, thence from the light on Fisherman Shoal through the eastern edge of Pilot Island to intercept the Door Peninsula.

District WM-3 is bounded on the west by WM-2, on the north and east by the Wisconsin-Michigan boundary, and on the south by an extension of the Door-Kewanee county line to an intersection with the interstate boundary.

District WM-4 is bounded on the north by WM-3, on the east by the Wisconsin-Michigan boundary, and on the south by an extension of the Manitowac-Sheboygan county line to an intersection with the interstate boundary.

District WM-5 is bounded on the north by WM-4, on the east by the Wisconsin-Michigan boundary, and on the south by an extension of the Milwaukee-Racine county line to an intersecsection with the interstate boundary.

District WM-6 is bounded on the north by WM-5, on the east by the Wisconsin-Michigan boundary, and on the south by the Wisconsin-Illinois boundary.

LAKE HURON AND ADJOINING WATERS

INTERNATIONAL BOUNDARY

The boundary between Canada and the United States in Lake Huron and North Channel is a line between the following turning points established by the International Boundary Commission:

Turning point number 215 - latitude 43°00'41", longitude 82°24'50"
Turning point number 216 - latitude 43°35'28", longitude 82°07'22"
Turning point number 217 - latitude 45°20'19", longitude 82°31'07"
Turning point number 218 - latitude 45°49'16", longitude 83°35'50"
Turning point number 219 - latitude 45°59'53", longitude 83°26'02"
Turning point number 220 - latitude 46°06'21", longitude 83°34'19"
Turning point number 221 - latitude 46°07'18", longitude 83°39'18"
Turning point number 222 - latitude 46°06'10", longitude 83°45'36"

ST. MARYS RIVER
Mackinac Bridge
NC-1
Knight Pt.
LITTLE CURRENT
Badgeley I.
Bad River Pt.
Barrie I.
NC-2
NC-3
Drummond I.
Cockburn I.
MANITOULIN ISLAND
Northwest
Burnt I.
MH-1
OH-1
Prarie Pt.
Dawson Rock
GB-1
CHEBOYGAN
Hungerford Pt.
Lonely I.
Fitzwilliam I.
Yeo I.
Cove I.
GB-3
Adams Pt.
MH-2
OH-2
GB-2
SAUGEEN
Western I. Light
Moose Deer Pt.
Surprise Shoal
Cape Dundas
GB-4
BLACK RIVER
MH-3
OH-3
PENINSULA
Au Sable Pt.
MH-4
Pt. Clark
Pt. Aux Barques Light
SAGINAW BAY
MH-5
LAKE HURON
OH-4
DISTRICT BOUNDARY
INTERNATIONAL BOUNDARY
BAY CITY
RICHMONDVILLE
MH-6
GRAND BEND
10 5 0 10 20 30 40
Statute Miles
OH-5
PORT HURON
SARNIA

Turning point number 223 - latitude 46°07'08", longitude 83°49'35"
Turning point number 224 - latitude 46°03'38", longitude 83°54'13"
Turning point number 225 - latitude 46°03'24", longitude 83°57'20"
Turning point number 226 - latitude 46°06'09", longitude 83°58'35"

STATISTICAL DISTRICTS

Michigan

District MH-1 in Lake Huron and North Channel is bounded on the west by the Mackinac Bridge, on the north and east by the international boundary to the St. Marys River, and by a line from Adams Point northeasterly to an intercept with the international boundary at right angles.

District MH-2 is bounded on the west by MH-1, on the north and east by the international boundary, and on the south by a line true east from the mouth of the Black River to an intersection with the international boundary.

District MH-3 is bounded on the north by MH-2, on the east by the international boundary, and on the south by a line true east from Au Sable Point to an intersection with the international boundary.

District MH-4 is bounded on the north by MH-3, on the east by the international boundary, and on the south by a line from Point Aux Barques Light on a true azimuth of 57° to an intersection with the international boundary.

District MH-5 is bounded on the north by MH-4, on the east by the international boundary, and on the south by a line true east from Richmondville, Michigan, to an intersection with the international boundary.

District MH-6 is bounded on the north by MH-5, and on the east by the international boundary.

Ontario

District OH-1 in Lake Huron is bounded on the west and southwest by the international boundary, on the southeast by a line from Hungerford Point southwesterly to turning point No. 217 of the international boundary (latitude 45°20'19", longitude 82°31'07") west of the opening of Georgian Bay, and on the north by a line across the narrowest part of the channels between Drummond and Cockburn Islands east of the international boundary, and between Cockburn and Manitoulin Island.

District OH-2 is bounded on the north by OH-1, on the east by a line from Hungerford Point to the northwest tip of Fitzwilliam Island, thence through the narrowest channels between Fitzwilliam, Yeo, Cove, and Russel Islands, and the Saugeen Peninsula to the south, on the west by the international boundary, and on the south by the 45th parallel.

District OH-3 is bounded on the north by OH-2, on the west by the international boundary, and on the south by a line true west from Point Clark to an intersection with the international boundary.

District OH-4 is bounded on the north by OH-3, on the west by the international boundary, and on the south by a line true west from Grand Bend, Ontario, to an intersection with the international boundary.

District OH-5 is bounded on the north by OH-4, and on the west by the international boundary.

District NC-1 in the North Channel is bounded on the west and southwest by the international boundary, on the south by OH-1, and on the east by a line from Knight Point true south to Barrie Island.

District NC-2 is bounded on the west by NC-1, and on the east by the bridge at Little Current, Ontario.

District NC-3 is bounded on the west by the bridge at Little Current, Ontario, and on the east by a line running from Prairie Point easterly to the southwest point of Northwest Burnt Island, a line across the narrowest channel between Northwest Burnt Island and Badgeley Island, and a line true north from Underhill Point on Badgeley Island to an intersection with the peninsula to the north.

District GB-1 in Georgian Bay is bounded on the west by NC-3 and OH-2, and on the south and east by a line from the southern point of Fitzwilliam Island northeasterly through Dawson Rock to a point 3.75 statute miles beyond the marine marker stake on the rock, thence northeasterly to Bad River Point.

District GB-2 is bounded on the north by GB-1, on the west by OH-2, and on the south and east by a line from Cape Dundas northeasterly to the flashing light on Surprise Shoal, thence easterly 22.25 statute miles on a line that intercepts the navigation light in Western Islands, thence to the point 3.75 statute miles northeast of Dawson Rock (on the boundary of GB-1).

District GB-3 is bounded on the northwest by GB-1, on the southwest by GB-2, and on the south by a line from the point 22.25 statute miles easterly of Surprise Shoal light extending

easterly to the navigation light in Western Islands, thence northeasterly to Moose Deer Point.

District GB-4 is bounded on the north by GB-2 and GB-3.

LAKE ERIE

INTERNATIONAL BOUNDARY

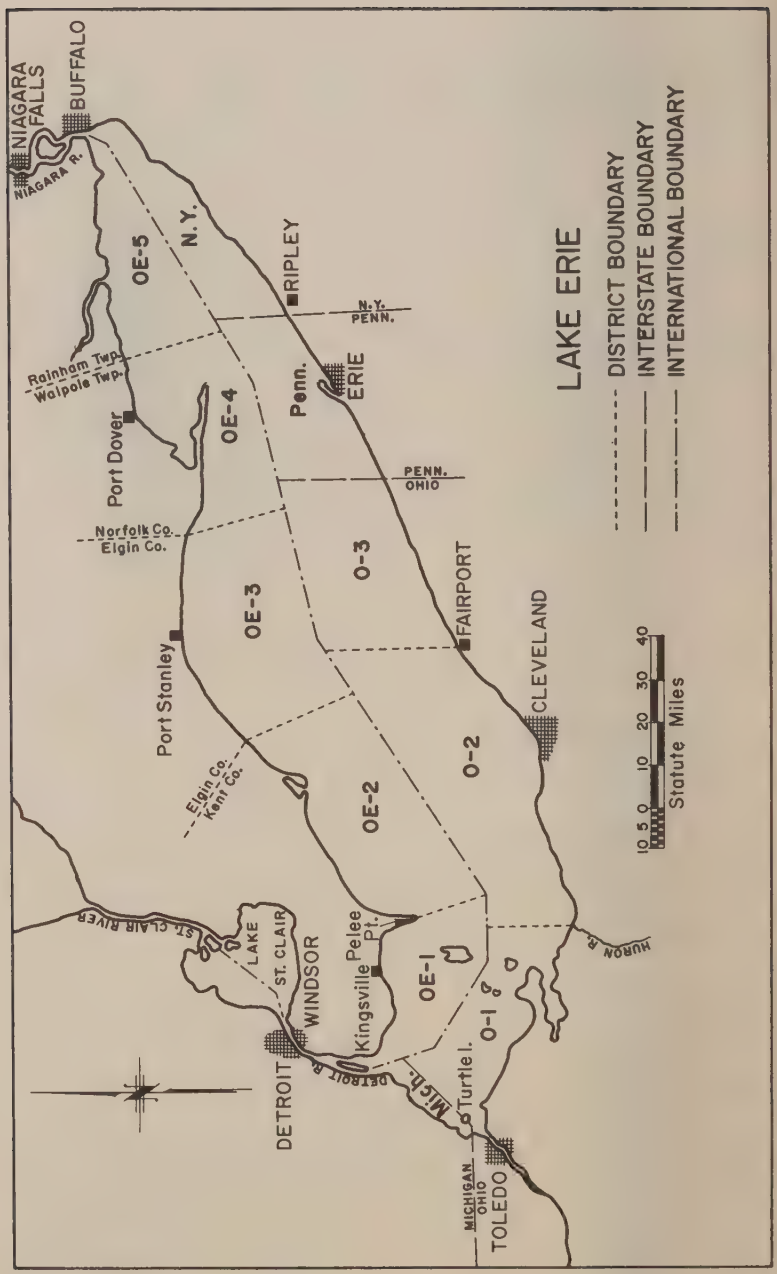
The boundary between Canada and the United States in Lake Erie is a line between the following turning points established by the International Boundary Commission:

Turning point number 152 - latitude 42°54'01", longitude 78°54'22"
Turning point number 153 - latitude 42°52'52", longitude 78°54'57"
Turning point number 154 - latitude 42°52'43", longitude 78°54'59"
Turning point number 155 - latitude 42°49'42", longitude 78°56'08"
Turning point number 156 - latitude 42°23'37", longitude 80°04'48"
Turning point number 157 - latitude 42°12'27", longitude 81°14'45"
Turning point number 158 - latitude 41°40'35", longitude 82°23'51"
Turning point number 159 - latitude 41°40'35", longitude 82°40'47"
Turning point number 160 - latitude 41°51'49", longitude 83°04'09"
Turning point number 161 - latitude 42°02'27", longitude 83°08'59"
Turning point number 162 - latitude 42°07'31", longitude 83°07'18"

INTERSTATE BOUNDARIES

Michigan-Ohio

Concurrent resolutions, passed by Legislatures of Michigan (Mich. Comp. Laws, Sec. 3.231) and Ohio (Ohio General Code Sec. 13855 and 13855-1) in 1945, described the boundary between the two states as a line passing through the center of the circular wall of the old lighthouse on Turtle Island on a true azimuth of 225° to an intersection with an extension of the land boundary between Michigan and


LAKE ERIE
DISTRICT BOUNDARY
INTERSTATE BOUNDARY
INTERNATIONAL BOUNDARY
Statute Miles
10 5 0 10 20 30 40
NIAGARA FALLS
BUFFALO
NIAGARA R.
OE-5
N.Y.
RIPLEY
N.Y.
PENN.
Rainham Twp.
Walpole Twp.
Port Dover
OE-4
Penn.
ERIE
PENN.
OHIO
Norfolk Co.
Elgin Co.
O-3
OE-3
FAIRPORT
Port Stanley
CLEVELAND
Elgin Co.
Kent Co.
OE-2
O-2
ST. CLAIR RIVER
LAKE
ST. CLAIR
WINDSOR
Pelee
Pt.
Kingsville
OE-1
O-1
HURON R.
DETROIT
DETROIT R.
MICH.
Turtle I.
MICHIGAN
OHIO
TOLEDO

Ohio to the southwest, and an intersection with the international boundary to the northeast. This resolution was rescinded by Michigan (Mich. Comp. Laws, Sec. 2.341) in 1947. The location of this boundary is, therefore, still undecided.

Ohio-Pennsylvania

The Ohio-Pennsylvania boundary in Lake Erie is a northward extension of the land boundary to its intersection with the international boundary (Penn. Statutes, Title 71, par. 1839).

Pennsylvania-New York

The Pennsylvania-New York boundary in Lake Erie is a northward extension of the land boundary to an intersection with the international boundary (Penn. Statutes, Title 71, par. 1861).

STATISTICAL DISTRICTS

Michigan

The Lake Erie waters of Michigan comprise a single statistical district.

New York

The Lake Erie waters of New York comprise a single statistical district.

Ohio

District O-1 is bounded on the west by the Ohio-Michigan boundary, on the north by the international boundary, and on the east by a line true north from the mouth of the Huron River to an intersection with the international boundary.

District O-2 is bounded on the west by district O-1, on the north by the international boundary, and on the east by a line true north from the entrance to Fairport Harbor to an intersection with the international boundary.

District O-3 is bounded on the west by district O-2, on the north by the international boundary, and on the east by the Ohio-Pennsylvania boundary.

Ontario

District OE-1 is bounded on the west and south by the international boundary, and on the east by a line from the southern tip of Pelee Point southeasterly to turning point No. 158 of

the international boundary (latitude 41°40'35", longitude 82°23'51").

District OE-2 is bounded on the west by OE-1, on the south by the international boundary, and on the east by a line from the Kent-Elgin county line to an intersection with the international boundary in line with the entrance to Fairport Harbor.

District OE-3 is bounded on the west by OE-2, on the south by the international boundary, and on the east by a line from the Elgin-Norfolk County line to an intersection with the international boundary in line with the junction of the Ohio-Pennsylvania boundary with the south shore.

District OE-4 is bounded on the west by OE-3, on the south by the international boundary, and on the east by a line from the Walpole-Rainham township line to an intersection with the international boundary in line with Ripley, New York.

District OE-5 is bounded on the west by OE-4, and on the south and east by the international boundary, and includes the Niagara River above the Niagara Falls.

Pennsylvania

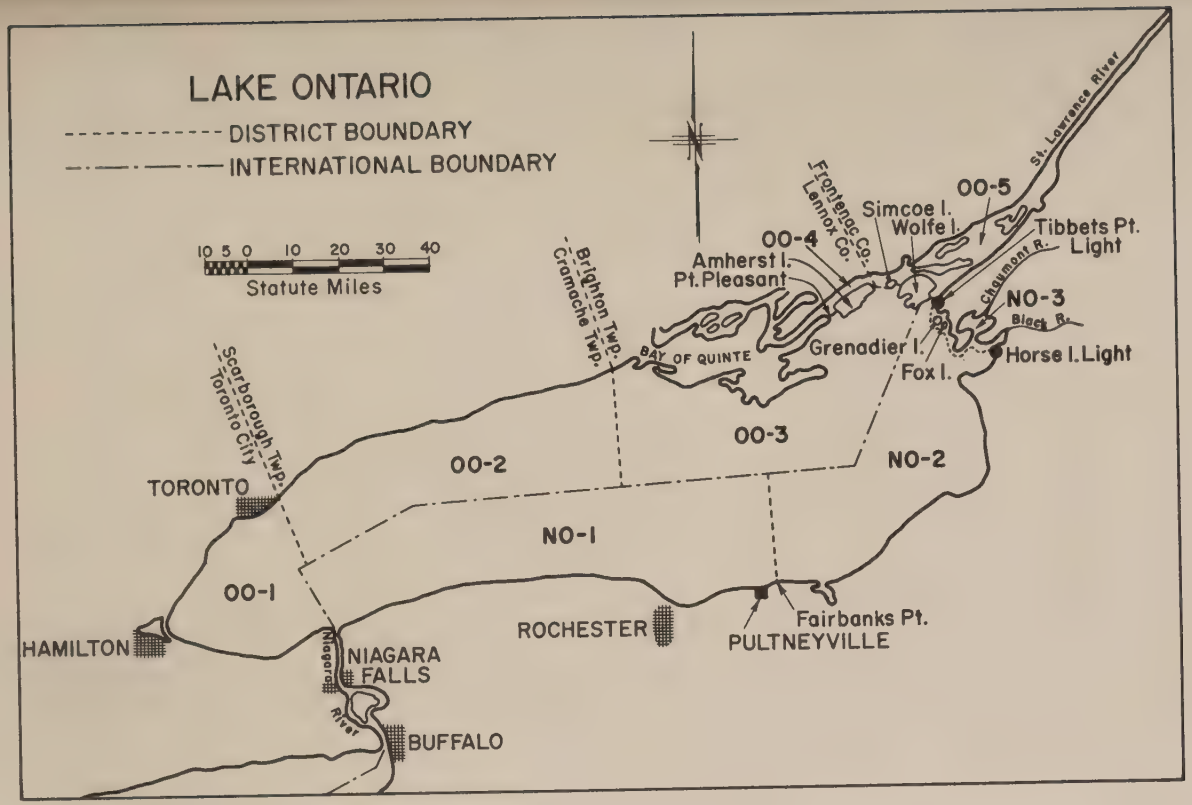
The Lake Erie waters of Pennsylvania comprise a single statistical district.

LAKE ONTARIO

INTERNATIONAL BOUNDARY

The boundary between Canada and the United States in Lake Ontario is a line between the following turning points established by the International Boundary Commission:

Turning point number 104 - latitude 44°08'03", longitude 76°21'11"
Turning point number 105 - latitude 44°05'38", longitude 76°26'21"
Turning point number 106 - latitude 43°37'52", longitude 76°47'49"
Turning point number 107 - latitude 43°37'52", longitude 78°41'26"
Turning point number 108 - latitude 43°27'02", longitude 79°12'03"
Turning point number 109 - latitude 43°15'44", longitude 79°04'14"


LAKE ONTARIO
DISTRICT BOUNDARY
INTERNATIONAL BOUNDARY
10 5 0 10 20 30 40
Statute Miles
N
St. Lawrence River
Frontenac Co.
Lennox Co.
Simcoe I.
Wolfe I.
OO-5
Tibbets Pt.
Light
Chaumont R.
OO-4
Amherst I.
Pt. Pleasant
Brighton Twp.
Cramache Twp.
NO-3
Black R.
Horse I. Light
Grenadier I.
Fox I.
BAY OF QUINTE
Scarborough Twp.
Toronto City
OO-3
OO-2
NO-2
TORONTO
NO-1
OO-1
HAMILTON
ROCHESTER
Fairbanks Pt.
PULTNEYVILLE
Niagara
River
NIAGARA
FALLS
BUFFALO

STATISTICAL DISTRICTS

New York

District NO-1 is bounded on the west and north by the international boundary, and on the east by a line true north from Fairbanks Point to an intersection with the international boundary.

District NO-2 is bounded on the west by NO-1, on the north by the international boundary, but on the east Chaumont Bay, Black River Bay and nearby shore waters that comprise district NO-3 are excluded.

District NO-3 includes the area within 1/2 mile of shore off Jefferson County between Horse Island Light on the south and Tibbets Point Light on the north, and including Black River Bay, Chaumont Bay, and Chaumont River west of Depauville, and waters within 1/2 mile of Fox and Grenadier Islands.

Ontario

District OO-1 is bounded on the east by the international boundary and by a line from the Toronto City-Scarborough township line to an intersection with the international boundary in line with the mouth of the Niagara River, and includes the Niagara River below Niagara Falls.

District OO-2 is bounded on the west by OO-1, on the south by the international boundary, and on the east by a line from the Cramache-Brighton township line to an intersection with the international boundary at right angles.

District OO-3 is bounded on the west by OO-2, on the south and southwest by the international boundary to the southern tip of Wolf Island, and on the north by the narrowest channel between Point Pleasant and Amherst Island, and by a line from the easternmost point of Amherst Island to the westernmost point of Simcoe Island, and the narrowest point of the channel between Simcoe Island and Wolfe Island.

District OO-4 is in the Bay of Quinte and bounded on the south by OO-3, and on the east by a line from the Lennox-Frontenac county line to the easternmost tip of Amherst Island.

District OO-5 is in the upper St. Lawrence River, including Lake St. Francis, bounded on the west by OO-3 and OO-4, on the south by the international boundary, and on the east by the Ontario-Quebec boundary. (Eastern extremity of this district not shown on map.)

Records of the Genetics Society of America, number 30, p. 111. (Abstract)
Also in Genetics, volume 46, number 8, p. 901.

SPRAGUE, LUCIAN M., Bureau of Commercial Fisheries, Biological Laboratory, Honolulu, Hawaii: *Erythrocyte antigens of the oceanic skipjack (Katsuwonus pelamis) recognized by phytoagglutinins.*—Saline extracts of leguminous seeds often have the property of agglutinating vertebrate erythrocytes. While many species of legumes yield extracts which agglutinate the erythrocytes of skipjack, five species, *Maackia amurensis*, *Virgilia capensis*, *Caragana arborescens*, *Glycine max*, and *Phaseolus vulgaris*, produce fluids which will recognize individual differences between skipjack bloods by agglutination procedures. Maackia extracts agglutinate all skipjack tested but following absorption by selected cells a fraction remains which exhibits an identical reaction pattern in comparison with Virgilia extracts.—In tests of 642 skipjack with extracts of the above seeds, four distinct patterns of reaction have been observed. Virgilia and Caragana permit the recognition of three phenotypes. Bloods agglutinated by Virgilia fail to react with Caragana. Bloods agglutinated by Caragana fail to react with Virgilia. Some bloods fail to react with either extract.—The patterns detected by Glycine and Phaseolus are apparently independent of one another and the Virgilia and Caragana patterns.—The relative proportion of the phenotypes recognized by Virgilia-Caragana and by Glycine are significantly related to the geographic origin of the samples.—A continuing study of the relative proportion of phenotypes in samples from different geographic localities in the central North and South Pacific Ocean is being made in an attempt to relate racial groups with marine ecology. Acknowledgment is made to PROFESSOR CHARLES COTTERMAN for the initial samples of seed.

Abstracts of Symposium Papers, Tenth Pacific Science Congress, p. 143.

SYMPOSIUM ON IMMUNOGENETIC CONCEPTS IN MARINE POPULATION RESEARCH

Studies on the Erythrocyte Antigens of the Skipjack Tuna (*Katsuwonus pelamis*)

LUCIAN M. SPRAGUE and LESLIE I. NAKASHIMA, U. S. Bureau of Commercial Fisheries, Honolulu Biological Laboratory, Honolulu, Hawaii, U. S. A.

At least five blood factors which form four systems of blood groups have been identified in the red blood cells of the skipjack tuna.

One, the C antigen, has been described by Cushing (1956). C-positive individuals are recognized by the action of natural bovine and ovine heteroagglutinins.

Four additional blood factors are now recognized by the use of saline extracts of legume seeds. Extracts of *Glycine max* detect A-positive bloods, extracts of *Phaseolus vulgaris* detect D-positive bloods, and extracts of *Virgilia divaricata* and *Caragana arborescens* detect two blood factors in the B system, Be and Bf. The relationships of Be Bf are not well understood except that they have mutually exclusive properties, Be-positive animals being Bf-negative and vice versa. About 20 to 30 per cent of the skipjack tested are Be-Bf-negative.

Of these reagents, those recognizing D-positive individuals and those recognizing Bf-positive individuals are not sufficiently definitive for use in population studies.

Reagents detecting C-positive, A-positive, and Be-positive animals, however, may be used to explicitly categorize skipjack erythrocytes. These reagents have been used in tests of 688 skipjack from the islands or island systems of Hawaii, Johnson, Christmas, Marquesas, and Rangiroa (Tuamotus).

When the frequencies of the occurrence of Be individuals from these areas were compared, the relative proportion of Be individuals sampled near Rangiroa was clearly distinct from the frequencies of Be from all other areas sampled ($P<.001$; *z*-test).

The sample from the Marquesas Islands is different from all other areas with respect to the frequency of the occurrence of C-positive individuals ($.05<P<.01$; *z*-test).

On the contrary, samples taken from Hawaii, Christmas, and Johnson Islands exhibit marked homogeneity in the frequencies of the characters A,C, and Be. These data indicate the occurrence of at least two reproductively isolated stocks of skipjack in the areas sampled.

Further studies are inprogress which will attempt to delineate the range and character of these stocks in greater detail.

RAPID COUNTING OF NEMATODA IN SALMON BY PEPTIC DIGESTION

by

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and

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ABSTRACT

The nematode parasite *Anisakis* sp. can be recovered, relatively unaltered, from chum salmon musculature by high temperature (52°±2°C.) peptic digestion of the flesh. The procedure, which is presented in detail, appears to be more thorough in isolating the parasite than dissection of the flesh and manual isolation of the worms. In addition, the procedure is rapid, comparatively simple, economical, and suitable for the examination of large numbers of samples.

The population of *Anisakis* sp. larvae in chum salmon appears to be concentrated in the ventral section of the fish, that is, below the lateral line, which suggests that only the ventral quarters of the fish need to be examined for estimating infection intensity.

INTRODUCTION

A major problem in the management of the international North Pacific salmon fishery is the resolution of a line or corridor in the North Pacific Ocean which equitably divides high seas stocks of salmon according to their continental origin. One of the techniques for the characterization of the salmon stocks employs the use of naturally occurring parasites as indexes of racial likeness.

Among the more promising of the "tracer parasites" is the larval nematode *Anisakis* sp. Criteria for specific identification of *Anisakis* larvae are not well established. The species considered in this study may be one of several reputed species from fish-eating mammals. The larvae in salmon appear to be morphologically identical with those in herring. Furthermore, the ecological backgrounds of herring and salmon have much in common to support a hypothesis of identity between these larval parasites. Bishop and Margolis (1955) considered the *Anisakis* larvae in herring (*Clupea pallasi*) from the coast of British Columbia to be the intermediate stage of *Anisakis simplex* (Rudolphi, 1809), a stomach parasite of whales and seals. Whatever the taxonomic status of these forms, there is no evidence to suggest that more than one species is represented in salmon.

The worms are colorless, translucent organisms which usually occur, to a greater or lesser degree, tightly coiled in lenticular cysts on serosal surfaces of visceral organs and in the somatic musculature of the salmon, within and between the myotomes. The difficulty of detection, recovery, and enumeration of these parasites in salmon musculature by the routine method of dissection and direct observation is a deterrent to a satisfactory rate of progress for thorough quantitative analysis of the infection phenomenon. Therefore, an investigation was undertaken to explore and develop other suitable methods of isolation and enumeration of the larval worms.

Various methods of chemical and enzymatic digestion of the host musculature were studied. Of these, only peptic digestion at relatively high temperatures proved efficient and economically suitable for use with large numbers of samples.

PROCEDURE

The fish are filleted and skinned. Each fillet is weighed to the nearest gram and then broken into several smaller pieces to increase initial surface area. The material from an individual fillet is placed in a digestion vessel (a beaker or jar of approximately 4 liters capacity). Five milliliters per gram of flesh of a 0.25 per cent pepsin solution (2.5 grams of granular pepsin, 1:10,000 made to 1 liter with 1 per cent HCl) are added to the vessel. The mixture is stirred gently, and

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Bulletin 3, Int. North Pac. Fish. Comm., January, 1961.

the pH is adjusted to 1.2 with concentrated HCl.

The digestion vessel is placed in a constant-temperature water bath or air oven where the temperature of the digestion mixture is raised to and maintained at the temperature optimum for the most rapid digestion (52°±2°C.). The digestion is permitted to continue for 15 minutes after the optimum temperature has been attained. During the heating and holding periods, the mixture is stirred mechanically at a moderately high speed using a glass stirring rod.

Following the holding period, the mixture is permitted to stand at room temperature for 5 minutes without agitation. During this period, the peptonized tissue forms a layer at the top of the solution, and the worms settle to the bottom. The layer of peptonized material is decanted. The remaining liquid is agitated to suspend the worms and then filtered through a standard 80-mesh grading sieve. The residue on the screen is washed several times with cold water and then transferred to a large Petri dish to which are added a few milliliters of 10 per cent formaldehyde.

The formaldehyde further denatures the proteinaceous components and causes the worms to appear opaque and whitish in color, suitable for rapid enumeration against a dark background.

EVALUATION OF THE PROCEDURE

The relative efficiencies of recovery of the parasites by the dissection method and by the peptic digestion procedure first were evaluated. Thirty-nine chum salmon (*Oncorhynchus keta*), obtained from various areas of the North Pacific Ocean, were used. The right sides of the fish were treated by dissection and manual isolation of the worms; the left sides by peptic digestion. The results of the study are presented in Table 1.

The data in Table 1 were analyzed statistically with the "t" test for the difference of mean values (Johnson, 1950). The population of worms isolated by dissection was found to be significantly less ($t=2.03$, $N=39$, significant at $P=0.05$) than that determined by the digestion procedure.

The possibilities existed that the difference might have been due to dissimilarities either in efficiency of recovery of the two procedures or in the distribution of the worms between the left and right sides of the fish. To determine which of these possibilities was most probable, a second study was initiated. In this study, 15 chum salmon were used. The parasites in both the right and left sides of each fish were first dissected and removed for enumeration. The dissected material then was treated by peptic digestion, and the residual entire worms in the flesh were isolated and counted. The data, which are independent of those in Table 1, are presented in Table 2.

A statistical analysis of the data, again using the "t" test for the difference of mean values, demonstrated that the number of parasites determined by the dissection method alone was significantly less ($t=3.26$, $N=15$, significant at $P=0.01$) than the total number counted, *i.e.*, the number determined by dissection plus the addi-

TABLE 1. ***Anisakis*** **sp. count by dissection and digestion.**

Sample No.	Count by dissection	Count by digestion	Sample No.	Count by dissection	Count by digestion
1	7	9	21	11	22
2	7	44	22	33	34
3	8	17	23	12	14
4	14	10	24	11	12
5	19	9	25	23	13
6	40	30	26	25	30
7	43	79	27	27	22
8	25	62	28	10	7
9	77	54	29	9	15
10	26	50	30	41	25
11	18	16	31	7	14
12	25	21	32	36	53
13	9	12	33	12	14
14	34	70	34	19	14
15	25	26	35	31	24
16	9	8	36	13	22
17	22	38	37	14	20
18	10	18	38	19	15
19	5	3	39	13	11
20	21	30			
			Total	810	987
			Mean	20.76	25.30

TABLE 2. ***Anisakis*** **sp. count by dissection, digestion of dissected material, and total count. (Summation of the two independent determinations)**

Sample No.	Count by dissection	Count by digestion of dissected portion	Total Count
1	18	0	18
2	25	2	27
3	51	5	56
4	16	3	19
5	57	2	59
6	100	17	117
7	67	6	73
8	6	2	8
9	6	1	7
10	34	4	38
11	22	6	28
12	9	1	10
13	3	3	6
14	0	0	0
15	11	1	12
Total	425	53	478
Mean	28.33	3.53	31.86

tional number recovered by digestion of the dissected material.

The mean difference between the total number counted and the number obtained by the dissection of the fish was taken as an approximation of a correction factor for data obtained by dissection. The correction factor was added to each of the individual dissection counts presented in Table 1, and an analysis of the corrected dissection data and the digestion data in Table 1 was carried out. This analysis (Table 3) demonstrated that a significant difference did not exist ($t = 0.50$, $N = 39$, not significant at $P = 0.05$) which indicated that the significant difference obtained with the uncorrected data in Table 1 was due to the difference in efficiency of recovery of the worms by the two methods rather than to differences in the distribution of the worms between the two sides of the fish.

It should be realized that the correction factor used in this analysis was merely a first approximation. A true correction factor probably would be a function of the number determined by the dissection procedure. The determination of an accurate factor would require more data than obtained in the present study.

Preliminary observations indicated that the population of *Anisakis* sp. larvae was concentrated in the musculature of the ventral section of the fish. Thirty fillets of chum salmon, each obtained from the right side of a fish, were divided along the lateral lines into dorsal and ventral sections. The sections were digested separately, and the number of worms in each of the sections was determined. The data, which are presented in Table 4, demonstrate the preponderance of worms in the hypaxial musculature.

TABLE 3. Correction of *Anisakis* sp. count of Table 1 using the correction factor as described in text.

Sample No.	Corrected dissection count	Count by digestion	Sample No.	Corrected dissection count	Count by digestion
1	10.5	9	21	14.5	22
2	10.5	44	22	36.5	34
3	11.5	17	23	15.5	14
4	17.5	10	24	14.5	12
5	22.5	9	25	26.5	13
6	43.5	30	26	28.5	30
7	46.5	79	27	30.5	22
8	28.5	62	28	13.5	7
9	80.5	54	29	12.5	15
10	29.5	50	30	44.5	25
11	21.5	16	31	10.5	14
12	28.5	21	32	39.5	53
13	12.5	12	33	15.5	14
14	37.5	70	34	22.5	14
15	28.5	26	35	34.5	24
16	12.5	8	36	16.5	22
17	25.5	38	37	17.5	20
18	13.5	18	38	22.5	15
19	8.5	3	39	16.5	11
20	24.5	30			
			Total	946.5	987
			Mean	24.26	25.30

TABLE 4. *Anisakis* sp. count by digestion method on dorsal and ventral portions of the sides of fish.

Sample No.	Total count	Dorsal count	Ventral count	Sample No.	Total count	Dorsal count	Ventral count
1	50	0	50	16	13	0	13
2	16	1	15	17	30	0	30
3	21	1	20	18	22	2	20
4	12	3	9	19	7	1	6
5	70	2	68	20	15	0	15
6	26	1	25	21	25	0	25
7	8	2	6	22	14	1	13
8	38	3	35	23	53	0	53
9	18	1	17	24	14	0	14
10	3	0	3	25	14	0	14
11	30	2	28	26	24	0	24
12	22	2	20	27	22	0	22
13	34	2	32	28	20	0	20
14	14	1	13	29	15	0	15
15	12	0	12	30	11	1	10
				Total	673	26	647
				Mean	22.43	0.86	21.56

DISCUSSION

The application of enzymatic proteolysis to the recovery of tissue-bound parasites has found considerable use in parasitology (Gustavson, 1953; Hoffman, 1955; among others). The successful use of enzymatic digestion in the case of nematodes undoubtedly depends upon the resistance of the cuticle to the proteolytic attack of the specific enzyme used. The resistance is due to the collagenous nature of the cuticle as demonstrated by Chitwood (1936) and more recently by Bird (1957).

In all cases of which the authors are aware, the enzymatic digestion techniques have been pointed toward recovery of living parasites for subsequent use in morphological, physiological, or infectivity studies. Under these conditions, enzymatic digestion of the investing tissue must be carefully controlled, lest the physical conditions of the system, notably temperature and hydrogen-ion concentration, exceed the tolerance of the parasite in question. The enzymes pepsin and trypsin, for example, most typically are used in solutions maintained at temperatures not exceeding 37° or, at a maximum, 39°C., which are temperatures that are obviously optimal, or nearly so, for all animal parasites potentially infective, at the stage of recovery, for homothermous hosts. In the event that it is known or assum-

ed, *a priori*, that the parasite is infective for a poikilotherm, the temperature of the digest solution is changed accordingly.

The present investigation concerns the use of peptic digestion in extensive quantitative studies which are not concerned with the recovery of viable parasites. Under the conditions of present investigation, certain advantages are evident in what may be termed high-temperature peptic digestion. Economy was important, and therefore the use of minimal concentrations of enzyme was desired. In addition, time for quantification was considered of utmost importance.

For enzyme reactions, time and temperature are interdependent variables. The actual temperature at which an enzyme reaction proceeds at a maximum rate depends on many factors such as the purity and concentration of the enzyme and substrate, the presence of activators or inhibitors, and the method of following the reaction. As has been well established (Baldwin, 1953; Neilands and Stumpf, 1955), the so-called optimum temperature is a function of the time chosen for rate measurement. For any given set of experimental conditions, it is possible to determine the temperature at which the greatest amount of chemical change is catalyzed by an enzyme under that particular set of conditions. Owing to the susceptibility of enzymes to thermal inactivation, at temperatures lower than the optimum the enzyme will be relatively more stable and the reaction will proceed more slowly but will continue longer, resulting in greater concentrations of end products. At temperatures greater than the optimum, the reaction will proceed more rapidly, but the catalytic properties of the enzyme will be more rapidly destroyed (Baldwin, 1953).

A series of experiments were carried out to determine the optimum temperature for peptonization which would require a minimum of time and a minimum of enzyme concentration. The results of these experiments demonstrated that with 5 milliliters of 0.25 per cent pepsin solution per gram of flesh, 15 to 20 minutes at 50°–54°C. was sufficient for peptonization of the flesh and complete separation of worms from the musculature. At successive temperatures lower than 50°C., the time for complete peptonization was lengthened so that it prohibited accumulating mass data; at successive temperatures greater than 54°C., thermal inactivation of the enzyme interfered with the digestion.

In addition to the simplicity and rapidity of the method, the high-temperature digestion procedure is efficient in that the worms are easily recognized, and recovery of all the larvae is facilitated. Furthermore, personal error and fatigue are not likely to affect the results as much as in the case of the more tedious procedure of dissection and manual isolation.

The procedure is economical in that the necessary equipment is simple and inexpensive. The principal cost is that of pepsin, which was found to average slightly less than $0.0005 per gram of flesh digested. In the present investigation, the fish were small, and the average weight of the fillets was 400 grams; the cost of pepsin per fillet was $0.20, or $0.40 per fish. If only the ventral portions of the fillets had been used for the enumeration studies, the cost per fish would have been approximately $0.18.

The procedure also offers the advantage that it lends itself to multiple determinations. During the course of the investigation, it was found that 2 people, working with a total of 5 digestion vessels, could prepare the necessary solutions and treat and enumerate the parasites in 50 fillets during a normal working day. Thus, a single operator can examine four times as many fish in a unit of time as with the dissection method.

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Printed in U. S. A.

LARVAL CARAPID FISHES FROM HAWAII, WITH REMARKS ON THE ECOLOGY OF ADULTS.—Midwater trawling ten miles off Waianae, Oahu, Hawaiian Islands, from the U. S. Bureau of Commercial Fisheries research vessel *Hugh M. Smith*, resulted in the capture of one vexillifer and two tenuis larval stages of the family Carapidae. The vexillifer is 64 mm in length and the tenuis 157 and 200 mm. Attempts to identify these larval pearlfish with their respective adult forms led to a brief examination of the biology of this family as represented in Hawaii.

Gosline and Brock (*Handbook of Hawaiian fishes, p. 280,* 1960) record *Snyderidia canina* Gilbert, *Encheliophis gracilis* (Bleeker), *Carapus margaritiferae* (Rendahl), and *Carapus homei* (Richardson) from Hawaii. Their material has been seen, with the exception of *Snyderidia,* along with additional adult specimens from the Bureau of Commercial Fisheries collections. Thanks are due Dr. W. A. Gosline, University of Hawaii. for the loa'ı of his material, and Dr.

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D. C. Arnold, College of the Venerable Bede, for opinions on identification.

With only four carapids known from Hawaii, the problem of relating the larval and adult stages was not particularly difficult. There is, however, the possibility of the larvae being the young of an unknown adult. The fact that the anal fin commenced anterior to the dorsal fin eliminated *Snyderidia* from consideration, while pectoral ray counts of 19–20 and anal ray counts of 196–241 eliminated *Carapus margaritiferae,* the adults of which have 13–14 pectoral and 161–163 anal rays. To determine whether the young were *E. gracilis* or *C. homei,* attention was turned to the morphology of the lower jaw, as illustrated by Arnold (*Bull. Brit. Mus. Nat. Hist. 4(6):256, 1956*). In *homei* the lower jaw is high posteriorly and bears a long bony ridge laterally, while in *gracilis* it is low posteriorly and lacks the ridge. My tenuis larvae have the jaw structure of *homei* and are referred to that species. That this is probably correct has been confirmed by D. C. Arnold (personal communication). The vexillifer, unfortunately, is damaged and cannot be identified as confidently. Its 203 anal rays fall within the 195–206 range found for adult *homei* rather than the 172–180 range found for adult *gracilis,* but it should be borne in mind that there is attrition of the tail tip in adults and these ranges may not be applicable to all size groups.

Fig. 1 shows the changes in gross morphology accompanying the transition from a pelagic to an inquiline mode of life for *C. homei.* Of note are the shrinkage in length, thickening in cross section, and increase in head size. A similar succession of events has been shown for *C. acus* by Padoa (*Pub. Staz. Zool. Napoli 20(2):111–21, 1947*).

Ecological data are available for the adults of three of the four species of Hawaiian Carapidae. Three *Encheliophis gracilis,* 192–237 mm in length, were obtained from the common sea cucumber, *Holothuria atra.* Two fish had gorged on the gonads of their hosts, the viscera of which were otherwise intact, while the third fish contained nothing in its stomach and was found in an eviscerated host. It appeared that the fish fed by swallowing the free ends of the attenuate gonad and working forward to the attached base. Parasitism on host gonads may be a general phenomenon for those species inhabiting holothurians, as it has been recorded for *Carapus acus* (Arnold, *Pub. Staz. Zool. Napoli 24(2): 160, 1953*). It cannot be a serious menace to the Hawaiian sea cucumber population, however, for *H. atra* is common on reefs whereas pearlfish are rare. Of 122 holothurians (114 *H. atra,* 4 *H. cinerascens,* and 4 *Actinopyga mauritiana*) dissected by the writer, only two contained fish. Dr. S. J. Townsley, University of Hawaii, has informed me that he found no pearlfish in 702 sea cucumbers palpated, but not dissected, in a search for commensal crabs. Of this total, 433 were *atra,* 208 were *mauritiana,* 8 were *cinerascens,* and the balance represented seven less common species. A similar paucity of pearlfish has been noted by Parker (*Proc. Nat. Acad. Sci. Wash. 12(7):421–2, 1926*) and Aronson and Mosher (*Anat. Rec. 111(3):489, 1951*) for the Florida-Bahamas region.

Four *Carapus homei,* 80–121 mm in length,

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were removed from the body cavities of cushion stars, *Culcita novaeguineae.* In contrast to the hosts of *E. gracilis,* which were obtained at depths of 1–6 feet, the starfish harboring *C. homei* were collected at 40–70 feet. The starfish were not abundant and were not systematically sampled for pearlfish, but it was noted that two fish sometimes occupied the same starfish. The stomachs of these inquiline *homei* were empty. The tenuis and vexillifer larvae of *homei* mentioned above were captured within 450 feet of the surface in water 8000 feet deep, the time of day being 8–10 P.M. Thus, contrary to Arnold's statement (1956), these larvae were epipelagic rather than benthic.

Four *Carapus margaritiferae,* 60–73 mm in

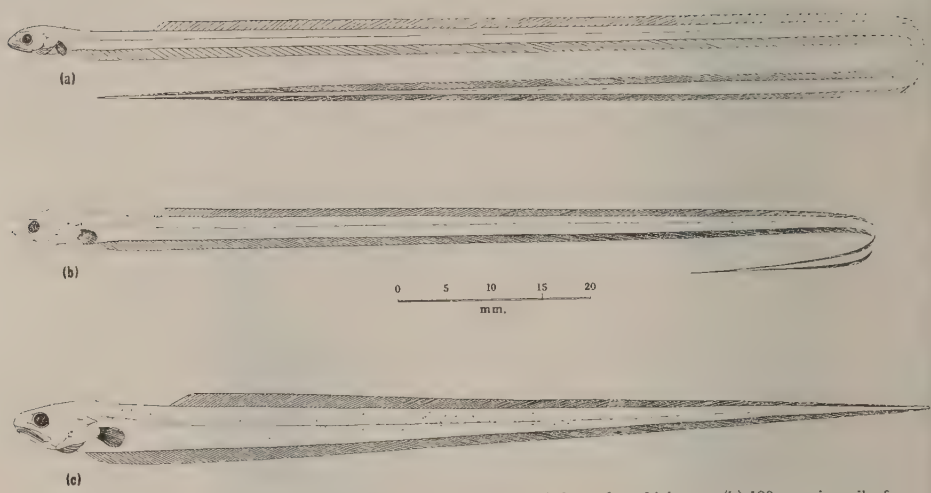

Fig. 1. Larval and juvenile stages of *Carapus homei*. (a) 200 mm. tenuis larva from high seas, (b) 120 mm. juvenile from *Culcita*, (c) 97 mm. juvenile from *Culcita*. The small protuberance anterior to the dorsal fin of the tenuis larva is the persistent vexillum base.

length, were available for study. One was found among the viscera of the rock oyster *Chama iostoma*, another from an unspecified oyster, and host data are not available for the other two. None contained food in the digestive tract, so that the diet of this remarkably toothed species remains unknown.—Donald W. Strasburg, *United States Department of the Interior, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.*

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DONALD W. STRASBURG

DIVING BEHAVIOUR OF HAWAIIAN SKIPJACK TUNA

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Diving Behaviour of Hawaiian Skipjack Tuna

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Introduction

The principal commercial fishery in Hawaii is for oceanic skipjack, *Katsuwonus pelamis* (Linnaeus), a surface-schooling tuna 40–90 cm in length which is captured exclusively by day using pole-and-line with live-bait as chum. In an attempt to increase the catch per unit of effort, the Honolulu Biological Laboratory (HBL), U.S. Bureau of Commercial Fisheries, has begun studies of skipjack behaviour. Major aspects of this subject have been investigated from an underwater observation chamber mounted on the research vessel "Charles H. Gilbert". This blister-like structure, which has been described by STRASBURG and YUEN (1960), is located two metres below the surface in the fishing area at the ship's stern. From this vantage point it is possible to study skipjack behaviour during fishing and at other times.

During July–September 1959, the "Charles H. Gilbert" was engaged in experimental skipjack fishing in Hawaiian waters. Experiments consisted of varying certain fishing conditions such as kind and amount of bait, bait supplements, etc., and in addition to such tests, collecting general information on the behaviour of skipjack. One conspicuous behaviour pattern observed during skipjack fishing was an abrupt vertical movement which we have called "diving". Diving consisted of skipjack vanishing from view in a nearly vertical direction, the fish disappearing at 30–60 m depths. This is of practical importance to the fisherman, for a school which dives frequently requires more bait and yields a smaller catch than a school which remains at the surface.

This report describes a possible cause of skipjack diving. Attention was focused on prey organisms because preliminary observations indicated a relation between prey and behaviour. For example, the fishermen believe that skipjack are conditioned to their natural food, and are difficult to catch with baits differing greatly from this food. In order to evaluate the feasibility of fishing a particular school they examine the spewings of the first few fish caught. The results of their examinations may be used to determine fishing procedure

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or to rationalize a poor catch. If the regurgitated material contains numerous postlarval synodontid fish, the fishermen believe that few skipjack will be caught and extensive bait expenditure is unwarranted.

Methods

Test fishing on the "Charles H. Gilbert" consisted of alternate periods of normal and experimental routine which allowed observers to compare skipjack behaviour under constrasting conditions. Although frequently affecting catch and catch rate, none of the tests caused the tuna to dive, and test effects are therefore ignored in the following account. Records of tuna activity consisted of underwater motion pictures, recorded oral comments by underwater and surface observers, and records of time and catch. Echo-sounders were not used to record skipjack activity primarily because these fish lack a swim-bladder and thus give poor echoes. After fishing, meteorological and water temperature data were obtained, and a sample of the catch was examined for length, sex, and food consumed.

Stomach contents were usually determined for a sample of ten skipjack, but a larger number was examined when an unusual diet was indicated. Dietary items were counted and a rough attempt made to judge their volumes. Excluding bait, 42 food items were encountered, but only ten of these occurred frequently. One of these, unidentified fish remains, was not considered further, but an idea of the importance of the others can be obtained from Table 1.

Identification of the more important food items was necessarily based on the specimens in best condition, and there is a possibility that other species occurred in the damaged material. Fish being eaten were postlarval *Acanthurus* spp. (Acanthuridae), postlarval *Chaetodon corallicola* Snyder (Chaetodontidae), juvenile *Holocentrus lacteoguttatus* Cuvier and Valenciennes (Holocentridae), juvenile *Parupeneus* sp. (Mullidae), and postlarval *Synodus variegatus* (Lacepède) (Synodontidae). Because these fish are littoral as adults, some interest is attached to the fact that their larval and juvenile stages are pelagic. It is thus desirable to explain the procedures used in identification and to briefly describe the specimens.

Acronurus-stage Acanthuridae were identified with the aid of RANDALL's publications (1955, 1956). Meristic characters were used to determine the silvery 25–33 mm chaetodontid postlarvae. Their formulae of dorsal rays XIII, 21 to 23 (usually 22); anal rays III, 18 or 19; pectoral rays 15; and scale rows 31 to 33 are referable only to *Chaetodon corallicola* among the Hawaiian butterfly fishes (GOSLINE and BROCK, 1960; WOODS, in SCHULTZ. *et al.*, 1953; and personal examination of specimens). The squirrel fish were all *Holocentrus lacteoguttatus* (WOODS, in SCHULTZ, *et al.*, 1953; GOSLINE and BROCK, 1960); they were 54–58 mm in standard length, deep blue dorsally, silvery ventrally, and with a bright violet stripe separating these colours. The mullids were also blue and silver, and 53–58 mm in standard length. Four preserved mullids had a single row of caniniform teeth in each jaw and $2-\frac{1}{2}$ scale rows between the lateral line and the dorsal fin interspace. According to GOSLINE and BROCK (1960) they are therefore a species of *Parupeneus*. The descriptions by GIBBS (1959), GOSLINE and BROCK (1960), and SCHULTZ (in SCHULTZ, *et al.*, 1953) were used to identify synodontid postlarvae. The deep-lying dark spots as well as the

Table 1

Diet versus dive-frequency in skipjack

Station number	Number of dives: Dives ≥ 1 min.	Number of dives: All dives	Acanthuridae	Chaetodontidae	Holocentridae	Mullidae	Synodontidae	Crab megalops	Squid	Stomatopods	Empty
	Number of skipjack eating item (adjusted to sample size 10)										
45– 2	0	0	0	0	0	7	0	0	1	0	0
– 3	3	5	0	5·4	0	10	0	4·6	2·3	0·8	0
– 7	1	4	2	10	1	6	0	9	1	1	0
– 8	0	2	1	2	0	0	0	0	5	2	2
– 9	0	0	2	6	0	1	0	0	1	0	0
–23	3	3	0	5	0	0	0	0	0	1	2
–32	1	4	2	1	0	6	1	0	0	0	2
–33	1	2	6	9	1	1	2	1	9	4	1
–34	0	2	2	5	0	4	0	1	2	0	0
–35	1	3	6	10	3	6	2	0	6	4	0
–37	0	1	0	10	0	0	0	2	1·3	0·7	0
–38	1	1	0	10	0	0	1	0	0	1	0
–39	1	5	1	10	0	0	0	3	2	2	0
–44	1	2	1	5	0	2	0	1	3	1	2
–46	2	3	0	3·1	0·8	0	3·8	0	4·6	0·8	0·8
–47	1	1	0	0	0	4	0	0	3	0	5
–49	0	1	0	5	2	0	0	0	4	4	1
–50	5	7	0	2	3	0	4	0	8	0	0
–54	1	1	1	2	2	10	1	0	4	3	0
–57	0	1	1·2	0	0	0·6	0·6	5	1·9	8·8	0
–58	3	5	1	1	2	0	0	1	1	5	1
–59	1	3	0	0·7	3	9·3	0	0	0·7	0	0·7
46– 7	1	1	1·7	0	0	0	0	0	3·3	0·6	4·4
–10	6	8	2	0	9	1	2	0	5	1	0
r, all dives			0·036	−0·061	0·622[2]	−0·020	0·426[1]	0·160	0·242	−0·093	−0·228
r, dives ≥ 1 min.			−0·089	−0·233	0·681[2]	−0·101	0·518[2]	−0·089	0·294	−0·046	−0·087
% of stomachs containing item (305 stomachs examined)			10·5	36·7	9·8	27·5	6·6	10·8	27·9	17·4	12·1
% of schools eating item (27 schools sampled)			51·9	74·1	44·4	55·6	37·0	33·3	85·2	70·4	48·1

[1] Indicates a *p*-value between 0·05 and 0·01. [2] Indicates a *p*-value less than 0·01.

dentition of tongue and jaws showed the 12 preserved specimens to be *Synodus*; one specimen, at least, had the dorsal fin formula of *S. variegatus*. These postlarval lizardfish were large, 55–62 mm in standard length, and were eaten by skipjack captured 3–16 km from shore.

No attempt was made to identify the crabs megalops or stomatopods, but the squid were examined by Robert T. B. Iversen of HBL and identified as *Symplectoteuthis oualaniensis* (Lesson) and *Ommastrephes* sp., both of the family Ommastrephidae.

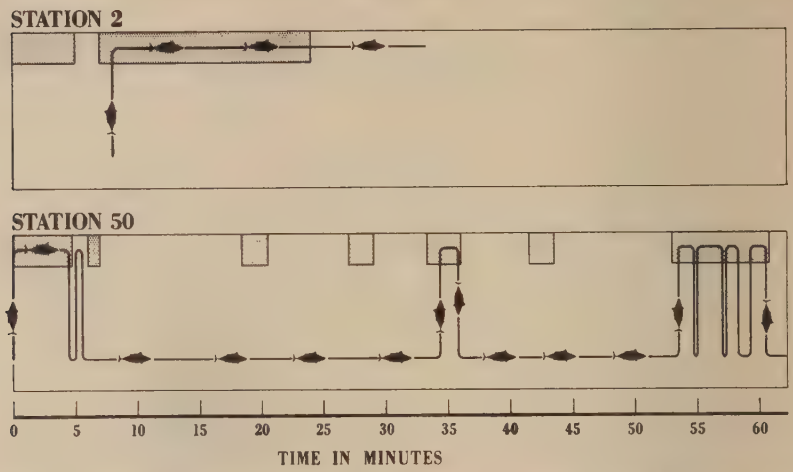

Figure 1. Activity of non-diving and diving schools of skipjack during fishing. Shaded blocks represent chumming intervals, fish figures indicate skipjack activity (surfacing or diving) during this period.

Relation of Diet to Diving

In the most desirable fishing situation a school of skipjack was attracted to the stern with live-bait (attracting fish with live-bait is locally known as chumming) and held there continuously for varying periods of time, usually about 20–30 minutes. With a diving school, the tuna were not only difficult to attract, but after fishing had begun it was periodically interrupted by the fish disappearing into the depths. Diagrammatic representations of extreme cases of these patterns of activity are given in Figure 1. Similar diagrams were prepared for all 24 schools observed in detail, and from these the number of dives per school was determined. A school which remained at the surface until the end of fishing was not considered to have dived, even though it departed in a dive after chumming stopped. Schools leaving the fishing area horizontally were also not considered to have dived, even if they emerged from the depths when re-engaged.

It was evident that diving was the rule rather than the exception (Figure 2). The number of dives per school ranged from 0 to 8, with a mean of 2·7. The tuna were away from the surface as briefly as 3 seconds or as long as 28 minutes. In the case of prolonged dives it was impossible to be certain that only one school was involved. It was felt, however, that only one was present, for the ship remained in the same spot and there were no indications (by birds or surface disturbance) of the approach of other fish. Thirty-three of the 65 dives observed resulted in a surface absence of one minute or more. Most dives were vertical or nearly so, and frequently the fish passed beneath the vessel as they descended. In nearly all cases diving was simultaneous among the hundred or more skipjack visible from the observation chamber.

As explained above, a sample of ten stomachs per school was examined for food. A few larger samples were proportionately reduced to ten for the sake of

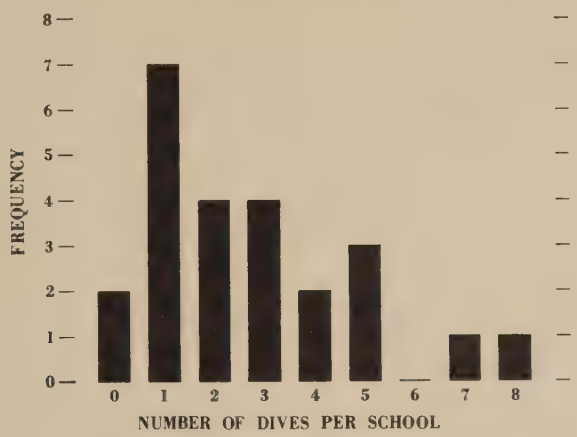

Figure 2. Frequency of diving in Hawaiian skipjack schools.

uniformity. The basic data, together with the results of the correlation analyses used to relate diet and dive-frequency are presented in Table 1. From this it is clear that the consumption of two foods, postlarval *Synodus variegatus* and juvenile *Holocentrus lacteoguttatus*, was significantly related to diving frequency. The correlation analyses treat each food item as if only it had been eaten, and therefore no particular account is taken of those cases, indicated in Table 1, in which *Synodus* and *Holocentrus* occurred together in skipjack stomachs.

Discussion

The food habits of Hawaiian skipjack have been discussed by Welsh (1949) and Yuen (1959), and are generally the same as those of skipjack of Japan (Suyehiro, 1938; Hotta and Ogawa, 1955) and the Philippines (Ronquillo, 1953). Wherever they occur, skipjack prey on small fish, squid, and crustaceans, taking a wide variety of species but also gorging on a few abundant forms. The heterogeneity of their diet has prompted Ronquillo (1953) to state: "These pelagic fishes are seemingly nonselective, that is, they are voracious eaters. They would eat any living organism available."

With such proclivities it is perhaps surprising to find skipjack behaviour influenced by a particular kind of prey. One example of this phenomenon is Yuen's observation (1959) that skipjack feeding on nomeids, thunnids, carangids, and gempylids (all relatively fast swimmers) are caught at a greater rate than skipjack preying on slower-swimming chaetodontids, scorpaenids, molids, and acanthurids. Similarly, skipjack feeding on nomeids, thunnids, and gempylids, but not carangids, are caught for a longer time interval than those eating the slower species.

Other observations on the susceptibility to capture of skipjack schools in relation to their natural food are less clear-cut with respect to diet-induced behaviour. Suyehiro (1938) found that skipjack preying on neritic organisms (mackerel, horse mackerel, spotted shrimp, amphipods, and crab larvae) were

relatively difficult to capture, whereas those taking oceanic food (flying fish, squid, and schizopods) were more easily caught. He surmised that this difference resulted from the relative abundance of food in neritic versus oceanic situations, rather than from a differential response to the food organisms.

It is unlikely that the consumption, *per se*, of *Synodus* or *Holocentrus* produces dyspepsia causing skipjack to flee the surface. Instead it is reasonable to think of them as diving in pursuit of deep-swimming prey whose attractiveness is greater than that of the chum. Thus, a school which is difficult to engage initially could be feeding on an enticing natural food, and one which dives after fishing has begun might be responding to natural food, or to other feeding skipjack, beneath it.

If better use is to be made of chum it is worthwhile to examine the characteristics of attractive natural food. In gross aspect there is little to distinguish *Holocentrus* from *Parupeneus*, the specimens recovered being of the same size, shape, and colour. They seem to have been equally available in 1959 (roughly half of the schools sampled had eaten each), although this is not always the case. YUEN (1959) found over three times as many schools eating holocentrids as mullids in 1956–57. Neither food seems to be preferred over the other, for although YUEN (unpublished data) found holocentrids in six times as many stomachs as mullids, the present data show holocentrids in one-third as many as mullids. Despite these vagaries, the fact remains that consumption of *Holocentrus* was associated with diving whereas consumption of *Parupeneus* was not. In addition to such possibilities as nonrandom sampling or a difference in the depth of occurrence of these two species, there is another possible explanation for this condition. This relates to prey behaviour, about which little is known, yet conceivably the "action" of *Holocentrus* might be attractive to skipjack whereas that of *Parupeneus* might not.

The other fish associated with diving, *Synodus variegatus*, is one of the few skipjack prey species having a prominent colour pattern. Whereas the other food organisms are inconspicuously colourless, blue, or silver, living *Synodus* postlarvae bear a series of large blackish spots on an otherwise unpigmented body. These markings are conspicuous to the human eye but do not suggest a fish-like form owing to the transparency of the intervening flesh. Instead an impression is given of an advancing file of disassociated spots. Judging from the dive data, skipjack detect and react to *Synodus* at distances on the order of 30 m. The immediacy of their response suggests triggering by some releaser, perhaps the spotted pattern of the prey. Apparently only a few *Synodus* are available to a skipjack school, for only 6·6 % of the stomachs examined in this study contained them, and YUEN (unpublished data) found them in only 10 of 573 stomachs. If these fish are as desirable skipjack food as they seem to be, then perhaps their characteristics can be put to human use. Mr. John C. MARR of HBL is presently examining the efficacy of skipjack lures having the shape and pattern of postlarval *Synodus*.

Summary

Observations from an underwater chamber showed that schools of skipjack commonly dive during fishing, leaving the surface for a minute or more on many occasions. Stomach analyses showed that the presence of two prey fish,

Synodus variegatus and *Holocentrus lacteoguttatus*, was significantly related to diving frequency. It was hypothesized that these two species were more attractive than the live-bait used by the fishermen, and that the skipjack dived in pursuit of them. A study of the characteristics of attractive natural food may lead to the development of better bait and lures for catching skipjack.

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ANDELSBOGTRYKKERIET I ODENSE

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BANDED COLOR PHASES OF TWO PELAGIC FISHES, *CORYPHAENA HIPPURUS* AND *KATSUWONUS PELAMIS*.—Banded color patterns in juveniles of pelagic fish species which do not, as adults, generally exhibit such patterns, have been recorded in the past, although not particularly commented upon. Observations of the last few years suggest that such patterns may also be common in the adults, but only while they are alive. Specifically, we wish to document the existence of banded color phases in living dolphin, *Coryphaena hippurus* Linnaeus 1758, and oceanic skipjack *Katsuwonus pelamis* (Linnaeus 1758).

One of us (Marr) observed banded dolphin off the west coast of Central America in the course of studies of the tropical tunas. An entry from his field notes for 17 March 1947 is: "At 0715 a small flock of boobies was seen working a school of bait. Upon approaching we could see a small school of bait. Larger fish breaking the surface slightly appeared to be dolphin (judging from their shape) but were banded; black bands alternating with greenish yellow ones! The bands were approximately 2" wide."

An entry of 11 April 1947 is: "At 0750 we came on a school of spinners [a species of porpoise] and yellowfin . . . We caught 252 yellowfin and three dolphin. One of the latter presented, while in the water, the same banded appearance previously noted. This was not discernible after the fish was brought aboard."

Both of these observations were made in the general area off Puntarenas, Costa Rica.

Two references to this phenomenon have been encountered in perhaps unconventional sources. One (Lamb and Cleveland, 1938. *Enchanted Vagabonds, p. 142*) relates to observations made in the general vicinity of Acapulco, Mexico: "Dolphins, to us, are the most beautiful fish in the sea. Their streamlined bodies are swift and graceful. They have a chameleon-like ability to change their color, turning from green to blue or brown, to yellow and brown stripes, their fighting colors."

The other (Hemingway, 1952. *The Old Man and the Sea, p. 79.*) refers to events in another ocean:

"I would like to fly very slowly at two hundred fathoms high and see the fish from above. In the turtle boats I was in the cross-trees of the mast-head and even at that height I saw much. The dolphin looked greener from there and you can see their stripes and their purple spots and you can see all of the school as they swim. Why is it that all the fast-moving fish of the dark current have purple backs and usually purple stripes or spots? The dolphin looks green of course because he is really golden. But when he comes to feed, truly hungry, purple stripes show in his sides as on a marlin. Can it be anger, or the greater speed he makes that brings them out?"

The other of us (Strasburg) has more recently had the opportunity to confirm the existence of this banded color phase in adult dolphin, and to extend our knowledge of its existence to adult oceanic skipjack. Observations of both species were made from an underwater viewing chamber, which has been described by Strasburg and Yuen (*J. Cons. Int. Explor. Mer*, In Press). This chamber is located near the stern of the U. S. Bureau of Commercial Fisheries' research vessel *Charles H. Gilbert*, and from it studies are being made of the feeding and schooling habits of pelagic fishes, principally Hawaiian skipjack. Motion pictures, still pictures and voice recordings provide the basis for subsequent analysis and also for the following account.

In July 1959, two large floating logs were encountered in Hawaiian waters, one a short distance off Waianae, Oahu, the other about 150 miles north of Nihoa. These logs were covered with sessile marine life and were closely accompanied by schools of small fish. Swimming around the logs were dolphin in surprisingly large numbers, 65 and 57 of which were ultimately landed after chumming with live bait. The length range of the captured dolphin was 620–1005 mm. More impressive than the number of dolphin was the variability of their color and color pattern. The ground color of various individuals was green, yellow, or silver, overlain with vertical bands or bars ranging from dark olive to black. In many individuals the bars were restricted to the head and trunk, the tail being the same color as the bars. In other fish, barring was uniformly distributed over the entire body, or sometimes completely lacking. A dolphin with at least three bars is shown in Fig. 1. Although difficult to detect from the photograph, the more anterior bars extend onto the dorsal fin membranes.

As noted above, the main use of the subsurface viewing chamber was for studying skipjack behavior, particularly their behavior during feeding. At such times large schools of skipjack were attracted to the ship's stern with live bait. Fig. 2 depicts a portion of such a school, and it is immediately apparent that skipjack, too, bear vertical bars. Bars were seen on fish weighing from 2 to over 30 pounds, but they were not always

Fig. 1. Banded color phase of the dolphin, *Coryphaena hippurus*.

Fig. 2. School of oceanic skipjack, *Katsuwonus pelamis*, showing both vertical bars and horizontal stripes.

observed on all members of a school. The effect of the viewing angle on the visibility of the bars is not known, but it is apparent that the presence or absence of the bars was under nervous control. Hooked fish bore the marks only briefly after leaving the water and lost all vestiges of them when moribund.

It is apparent (see Fig. 2) that the persistent, dark horizontal stripes are interrupted by light vertical bars, while the light horizontal stripes are

not interrupted by dark vertical bars. The transitory barred or banded appearance, then, is produced by light rather than dark bars. Presumably this is accomplished by the contraction of melanophores.

In addition to Hawaii, underwater observations were made of bars on skipjack in the Line Islands and off the west coast of Central America. It is likely that these marks are a regularly occurring feature which has not been recorded in photographs or paintings because of their evanescent nature and the general lack of underwater viewing facilities.

A cursory search of the literature and available photographs reveals that vertical bars are common among pelagic fishes. In addition to the ephemeral bands of adult *Coryphaena* and *Katsuwonus*, we note more or less permanent bars or bar-like rows of spots on adult *Neothunnus*, *Acanthocybium*, *Istiophorus*, *Makaira*, *Naucrates*, and *Ranzania*, and on juvenile *Coryphaena* and *Neothunnus*, among the more conspicuous pelagic forms. Because of the similarity in ecological position of most of these fishes, it is tempting to postulate an adaptive importance for the bars. To the submerged human eye they render the fish neither more nor less conspicuous, for the marks are only visible at short range, long after the fish has come into view. (When viewed from above the surface of the water they do, however, have the effect of presenting an unfamiliar pattern on a familiar silhouette, thus making sight identifications difficult). Whether bars have a communicative function between fish is a question to be answered only after more detailed observations than we have been able to make.—DONALD W. STRASBURG and JOHN C. MARR, *U. S. Bureau of Commercial Fisheries, Honolulu, Hawaii.*

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Contributions to the Study of Chesapeake Bay Striped Bass

COORDINATED BY
JAMES E. SYKES

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THE CHESAPEAKE BAY COOPERATIVE STRIPED BASS PROGRAM[1]

JAMES E. SYKES

ABSTRACT

The long-range objectives of coordinated research on the fishery, designed to assess the effects of fishing, are to estimate abundance, mortality rates, and exploitation parts of the striped bass, *Roccus saxatilis*, in Chesapeake Bay. The first phase, involving the cooperation of biologists of Maryland, Virginia, and the U. S. Bureau of Commercial Fisheries, was a pilot program of systematic tagging and recovery in 1957–8. The nature of further research on striped bass populations in Chesapeake Bay is described.

Introduction

During the 5-year period 1953 through 1957 the average annual commercial catch of striped bass, *Roccus saxatilis*, on the Atlantic coast was approximately 5,000,000 pounds and was valued at $1,000,000. The area of highest abundance was Chesapeake Bay where an average of 3,000,000 pounds was landed annually having a dockside value of $700,000. The pounds of fish caught in the bay by the sport fishery is not known, but observation has shown it to be among the larger of sport catches on the Atlantic coast.

Although the fishery is economically and recreationally important, many of the requisites for successful management are not yet known. Biological research on striped bass in Chesapeake Bay since the 1930's

[1] Contribution No. 173, Maryland Department of Research and Education, Solomons, Maryland.

dealt largely with age, growth, feeding habits, migration, and the location of spawning and nursery areas. Most of the programs were relatively small in scope and localized in area. In recent years the States of Maryland and Virginia recognized the need for population studies as a necessary aid in the management of their striped bass fishery. Estimates of abundance and mortality rates and the identification of separately exploitable components of the fishery were desired. The U. S. Bureau of Commercial Fisheries was requested by these states to lend support in a comprehensive striped bass research program.

A coordinated study was begun in 1957 to assess the effects of fishing upon Chesapeake Bay striped bass. The Virginia Fisheries Laboratory, the Maryland Department of Research and Education, the Maryland Department of Tidewater Fisheries, and the United States Bureau of Commercial Fisheries were research cooperators. The first phase of the study was a pilot program of systematic tagging and recovery in 1957 and 1958. It was designed for 1) determination of the seasonal location of striped bass by age classes; 2) development of a satisfactory tag and a tagging technique which would serve the purposes of the investigation; 3) location of sources of adequate tag recoveries from both sport and commercial fisheries to reflect quantitatively in subsequent studies the population or subpopulations available to the respective fisheries; and 4) evaluation, in addition to earlier meristic and tagging studies, of criteria for separating subpopulations in the bay.

Field data, collected cooperatively and in most events simultaneously, were pooled and members of the cooperating laboratories volunteered to analyze and report on phases of the research program. Results of the pilot tagging studies are given in the following sections of this report.

Lewis describes the methods employed in selecting the most satisfactory tag for the Chesapeake Bay program. Mansueti, and Massmann and Pacheco in two separate reports, interpret age, size, growth, sex, and migration of striped bass in relation to the fisheries of both Maryland and Virginia.

Since this portion of the study was completed, research dealing specifically with the population dynamics of the Potomac River striped bass has continued. This tributary supports the largest striped bass fishery in the area. Research is planned for the other major tributaries and the bay proper for determination of abundance, mortality rates, the existence of subpopulations, the contribution of stocks to other areas, and scientific methods of utilization.

All agencies involved have contributed as equitably as possible in their responsibilities of finance and manpower. The cooperation of state and federal personnel in this program has been outstanding and illustrates the results which can be obtained through the joint effort of laboratories having limited resources for conducting a large investigation.

Atlantic Coast Striped Bass Program, U. S. Bureau of Commercial Fisheries, Beaufort, North Carolina.

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Reduced Oxygen Tolerance and Toxicity of Petroleum Products to Juvenile American Shad

MARLIN E. TAGATZ

ABSTRACT

Experiments were conducted on juvenile American shad, *Alosa sapidissima*, to indicate tolerance to reduced oxygen, toxicity of petroleum products, and toxicity of petroleum products with accompanying low dissolved oxygen. All mortalities in reduced oxygen tests occurred at dissolved oxygen values of less than 2 ppm with lethal concentrations varying with the rate of reduction. No mortalities occurred when dissolved oxygen was maintained between 2 and 4 ppm. TL_m (median tolerance limit) values were determined for gasoline, diesel fuel oil, and bunker oil for 24- and 48-hour periods. Gasoline was the most toxic, fuel oil somewhat less toxic, and bunker oil least toxic. The lethality of petroleum products to shad was found to increase when accompanied by low dissolved oxygen.

Introduction

The commercial yield of American shad, *Alosa sapidissima,* on the Atlantic coast decreased from a peak of 50 million pounds in 1896 to a low of 8 million pounds in 1950. In certain coastal rivers, part of this depletion has been attributed to pollution and low oxygen content. Studies of shad in the Hudson and Delaware Rivers (Talbot, 1954:401–9; and Sykes and Lehman, 1957: 14–21) indicated that oil, domestic sewage, and industrial wastes had caused a reduction in the dissolved oxygen content of the water to a degree possibly detrimental to this species. Large numbers of young shad and herring died as a result of sewage pollution in the Delaware River near the Torresdale Pumping Station during the fall of 1950 (Fishing Gazette, 1950). Lane, et al. (1926:177) quoted the Commissioner of Fisheries of the Commonwealth of Pennsylvania, who said that surveys along the tidal section of the Delaware River indicated that oil and sludge from refineries and oil-carrying vessels were the main cause for the decline in numbers of shad in that region.

It has been established by various workers that oil pollutants are toxic to fish and marine invertebrates. Westfall (1943:5) found that goldfish became sluggish, lost equilibrium, and refused food when exposed to an oil effluent which was being discharged into the Buffalo River. Chipman and Galtsoff (1949) showed the toxic effects of oil on various forms of marine life. Roberts (1926) found that both gas oil and diesel oil were toxic to fish and attributed their toxic action to water soluble constituents and emulsions.

Studies were conducted on juvenile shad by the Bureau of Commercial Fisheries to indicate tolerance to reduced oxygen, toxicity of petroleum products, and toxicity of petroleum products with accompanying low dissolved oxygen. Investigations were exploratory and the results are considered indicative rather than definitive in application to the diverse conditions found in nature.

The American shad is anadromous, and sexually mature adults enter Atlantic coast rivers from the sea to spawn in late winter and spring. The young spend their first summer in the rivers (5 to 6 months) and then migrate to the ocean. In 3 to 6 years they reach sexual maturity and return to their native rivers to spawn. Shad of northern rivers that escape the fisheries spawn, return to the ocean, and are free to re-enter the river the following year provided they undergo no mortality. Those that spawn

in rivers south of Chesapeake Bay, and particularly south of North Carolina, die after spawning (Talbot and Sykes, 1958: 485).

Gerald B. Talbot, Director, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N. C., initiated this study, and the shad staff aided in collecting fish. Appreciation is expressed to G. E. Burdick, New York Conservation Department, and Charles M. Weiss, University of North Carolina, for reading the manuscript and for offering suggestions on treatment of the data.

Materials

Juvenile shad were obtained by seine from the Neuse River near New Bern, N.C., during September and October 1958–59. Fish were transported to the laboratory in a tank mounted on a truck as described by Sykes (1950). Suggestions by Doudoroff, et al. (1951) were followed in caring for and preparing test fish in the laboratory.

Three aquaria having glass sides were used in the experiments. Two aquaria served as experimental tanks and one as a control. The sides of each aquarium were covered with cardboard to shield fish from outside disturbance. In each test, 30 gallons (113.6 liters) of water from the seining site and 10 shad were placed in an aquarium. The specific gravity and pH of the experimental water ranged from 1.0028 to 1.0063 and from 7.4 to 7.6, respectively. Fork lengths of the test fish ranged from 55 to 72 mm (average length 66 mm) and weight ranged from 2.1 to 4.0 gms.

Methods

Four experiments were conducted in which dissolved oxygen was reduced to determine concentrations at which young shad could live and those which caused mortalities, and a fifth experiment was conducted to determine tolerance to low oxygen for a sustained period. Preliminary tests were made to resolve methods and obtain hypotheses for tests. Aquarium water was aerated to provide an initial dissolved oxygen of 7.0 ppm. Controls with oxygen maintained at or slightly more than 7.0 ppm were run simultaneously with these experiments.

Initial oxygen concentration was reduced by the test fish in open and covered aquaria. In the first and second experiments, reduction occurred slowly because of partial replacement of oxygen at the water surface from the atmosphere. In the third and fourth experiments, dissolved oxygen was reduced rapidly by covering the water surface with a layer of wax paper which prevented atmosphere-water exchange of oxygen. An experiment was terminated when a 50 per cent mortality occurred. Cessation of respiratory movement was considered as the criterion of death. In the fifth experiment, dissolved oxygen was reduced slowly by the test fish and maintained for 96 hours between 2.0 and 4.0 ppm. During this latter test, artificial aeration was required for short periods to maintain a minimum oxygen content of 2.0 ppm.

Water temperature and dissolved oxygen were determined at varying intervals (usually hourly after initial fish distress) during each experiment. Oxygen determinations were made using the micro-Winkler method as described by Welch (1948:211); a 25 cc sample of water was removed for each analysis from below mid-depth. Dissolved oxygen was 0.1 ppm greater in water at the surface of the aquarium than at mid-depth or bottom; however, the effect of this slight variation on the fish, which showed no depth preference, was considered insignificant.

Bio-assays were conducted to determine the toxicity of petroleum products to juvenile shad. The methods used were as prescribed by the Federation of Sewage and Industrial Wastes Sub-committee on Toxicity (Doudoroff, et al., 1951). Three series of experiments were conducted using regular grade gasoline (specific gravity 0.7953); grade No. 2 diesel fuel oil (specific gravity 0.8710); and Class C, grade No. 6 bunker oil (specific gravity 0.9698). Preliminary tests were made with different concentrations of each pollutant to determine the approximate range of toxicity. In the final experiments, the TL_m (median tolerance limit—concentration that causes 50 percent mortality) values were determined for 24- and 48-hour periods by straight line graphic

interpolation using semilogarithmic paper. A control free from pollutant was run concurrently with each test.

A measured quantity of pollutant was added to the surface of the water in each test. The water in each aquarium was circulated at a rate of 1 gallon per minute with an electric pump and ½″ diameter plastic tubing. Water was drawn from the bottom of the aquarium and diffused upon re-entry into the tank by flowing over an 8″ x 15″ perforated platform suspended directly above the surface of the water. Experimental water was therefore allowed to permeate the pollutant and extract any toxic water-soluble substances. The pattern of water circulation was an attempt to simulate current action and mixing of water under natural river conditions. In all experiments dissolved oxygen remained more than 6.0 ppm because of the method of water circulation.

Two experiments were conducted to determine the combined effects of low dissolved oxygen and petroleum toxicity on juvenile shad. In both tests the initial dissolved oxygen content of aquarium water was 6.5 ppm, and this was reduced at a rate of 1.0 ppm per 10 hours to 2.5 ppm by respiratory activity of the fish. In the first experiment, gasoline (68 mg/l) was then added to the surface of the water and in the second experiment, diesel fuel oil (84 mg/l) was added. The petroleum concentrations used were those in which no shad mortality occurred within 24 hours as determined in the bio-assay evaluation of the toxicity of these pollutants. The water in the aquarium was then circulated in the same manner as described in the petroleum toxicity tests. After the addition of oil, dissolved oxygen was maintained between 2.0 and 3.0 ppm for the duration of each test. To counterbalance an increase in oxygen caused by circulation of the water, compressed nitrogen was released into the aquarium using an air mist releaser. This method of decreasing oxygen is a physical process involving its dissolution from the aqueous phase into the gaseous phase in accordance with Henry's Law (Carpenter and Cargo, 1957:7). Dissolved oxygen was determined at approximately 10-minute intervals after addition of oil. Oxygen levels were maintained within the desired range by adjustment of nitrogen flow. Experiments were terminated after total mortality of test fish. A control free from oil and with oxygen maintained between 2.0 and 3.0 ppm was run in conjunction with these tests.

Free CO_2 and pH were determined at the beginning and end of each experiment. In the reduced oxygen studies, free CO_2 values were usually less than 5 ppm and never exceeded 10 ppm. Free CO_2 remained less than 3 ppm in the petroleum toxicity studies. The pH range in all tests was from 7.4 to 7.6, and water temperatures were between 21° and 23° C.

Results

Reduced oxygen experiments 1 through 4 (Table 1) revealed that when oxygen was reduced at a slow rate (1 ppm per 9½ and 11 hours), all mortalities occurred at less than 1.2 ppm, and when reduced at a more rapid rate (1 ppm per 3 hours), all mortalities occurred at more than 1.3 ppm. The fish remained schooled during the experiments until in distress. Individuals left the school at an oxygen concentration of 1.4 ppm when oxygen was lowered slowly, and at 2.4 ppm when lowered rapidly. Symptoms of distress were labored respiratory movements, violent gulping at the surface, sudden rapid swimming, and loss of equilibrium. Respiratory movements became more rapid as dissolved oxygen was reduced below 4.0 ppm. Fish surviving these experiments were in intense distress at the termination of each test.

TABLE 1.—Tolerance of juvenile American shad, *Alosa sapidissima*, to continuous reduction of dissolved oxygen, experiments 1–4.

Average rate of oxygen decrease from 7 ppm	Dissolved oxygen first mortality (ppm)	Hours elapsed	Dissolved oxygen 50% mortality (ppm)	Hours elapsed
1 ppm per 9½ hours	1.0	55.5	0.9	57.5
1 ppm per 11 hours	1.1	65.0	0.9	68.0
1 ppm per 3 hours	1.8	15.0	1.4	16.5
1 ppm per 3 hours	1.6	16.0	1.4	17.5

TABLE 2.—Tolerance of juvenile American shad, *Alosa sapidissima*, to sustained levels of reduced dissolved oxygen, experiment 5.

Dissolved oxygen[1] (ppm)	Hours maintained	Mortality
3.0–3.8	54	0
1.8–2.9	42	0

[1] Initially reduced from 7.0 to 3.8 ppm at a rate of 1 ppm per 12½ hours.

In experiment 5 (Table 2) juvenile shad were tolerant to dissolved oxygen maintained between 1.8 and 3.8 ppm for a 96-hour period. No distress except for more rapid than normal respiratory movements was noted among the test fish during this time. One death occurred in the controls run in conjunction with the reduced oxygen experiments. Other than this exception, control fish remained schooled and appeared in good condition.

In bio-assay studies on toxicity of petroleum products (Tables 3 and 4), gasoline, diesel fuel oil, and bunker oil were toxic to juvenile shad. The lighter petroleum products were comparatively more deadly than the heavier oils. Gasoline was most toxic, fuel oil somewhat less toxic, and bunker oil least toxic. A narrow critical concentration range (interval between highest concentration at which all fish survive for 48 hours, and the lowest concentration at which all die within 24 hours) occurred for gasoline. This range was between 68 and 114 mg/l. The toxicity of bunker oil was not sufficiently pronounced in this study to allow determination of the 24-hour TL_m using the highest concentration that could be properly tested. Concentrations of bunker oil greater than 2,500 mg/l formed a heavy oil layer on the surface of the aquarium which hindered water circulation.

The reaction of juvenile shad to toxic concentrations of each petroleum product was typically the same. Distress was first noted when individuals broke from the school to swim and probe at the surface. The fish next displayed loss of equilibrium by swimming inverted, tails down, on their sides, or with an arch in their bodies. Intensity and duration of distress varied with type and concentration of pollutant. The period from initial distress to death was within 1 hour with gasoline, 5 to 10 hours with fuel oil, and 12 to 18 hours with bunker oil. No mortality or distress occurred among control fish.

Specific concentrations of petroleum products and levels of reduced oxygen, found tolerable in these studies, were found to be lethal in experiments where they occurred together (Table 5). Distress and dispersion of test fish occurred 30 minutes after addition of gasoline and 120 minutes after addition of diesel fuel oil. After initial distress, mortalities occurred in 10 to 30 minutes with gasoline and in 60 to 180 minutes with diesel fuel oil. No deaths occurred in the

TABLE 3.—Survival of juvenile American shad, *Alosa sapidissima*, subjected to different concentrations of petroleum products for specified time intervals (10 fish used in each test).

Petroleum product	Concentration mg/l	Number surviving after		
		24 hours	48 hours	96 hours
Gasoline	152	0	0	—
	114	0	0	—
	99	2	2	—
	84	8	8	—
	68	10	10	—
	38	10	10	—
Diesel fuel oil	334	2	2	—
	251	3	2	—
	167	7	5	—
	125	8	7	—
	84	10	9	—
Bunker oil	2,417	8	5	2
	1,952	10	8	5
	1,580	10	9	7
	1,302	10	10	10
	837	10	9	9
	372	10	10	10

TABLE 4.—TL_m (median tolerance limit) values of gasoline, diesel fuel oil, and bunker oil for juvenile American shad, *Alosa sapidissima*.

Petroleum product	TL (mg/l)		
	24 hour	48 hour	96 hour
Gasoline	91	91	—
Diesel fuel oil	204	167	—
Bunker oil	—	2,417	1,952

ntrol where dissolved oxygen was maintained between 2.2 and 3.3 ppm for 5 hours. he control was maintained at more than 0 ppm for an additional 48 hours, and no elayed mortality occurred.

Discussion

The reduced oxygen experiments indicate at young American shad in unpolluted aters are able to acclimate to low oxygen oncentrations dependent on the rate of reiction. Shepard (1955:425, 430) found at in brook trout acclimation to low oxyen was accompanied by an increase in the bility of the fish to extract oxygen. This cclimation would aid fish to survive exosure to low levels of dissolved oxygen or short periods. The present study indiates that young shad can probably survive mited exposure to dissolved oxygen beween 2.0 and 4.0 ppm in natural waters here other environmental conditions are atisfactory. However, these low levels ver prolonged periods may not be adeuate for normal activity and growth and ay exert a deleterious effect when in comination or interaction with other unfavorble environmental stresses. In terms of a ingle standard, a minimum dissolved oxyen of 5.0 ppm has been established by Ellis, et al. (1947:12–3) and 4.0 ppm has een suggested by Burdick (1954:204) for he wellbeing of shad.

Ellis (1946) found less reduced oxygen olerance for juvenile American shad than hown in these experiments. Using 4-liter lasks containing one to five fish each, he ound that a mortality rate of approximately 49 percent occurred when dissolved xygen was reduced from 5.0 to 3.0 ppm at temperatures ranging from 20.2° to 22.5° C. Ellis reduced the oxygen level using a partial pressure apparatus at the rate of 1.0 ppm per 10 to 40 minutes. The method used and the rapidity of reduction probably account for the early mortalities.

The death-causing effects of petroleum products on juvenile shad were not ascertained in this study; however, loss of equilibrium exhibited by the fish indicated possible disturbance to the central nervous system. Ellis (1937:402), in classifying pollutants on the basis of locus of injury to the fish, stated in part that various volatile crude oil compounds can enter the body of fish through external structures such as gills and lining of the mouth. Gutsell (1921:7) stated that if a surface layer of oil is emulsified by agitation, it may coat the gill membranes of fish and cause death by suffocation. During the bunker oil tests, many small particles broke free from the surface oil layer and became suspended in the water. The gills of the fish examined at the termination of these tests were covered with many of these particles, which could have caused death by suffocation. From these limited studies, the cause of death from petroleum products appears to be in part physical and in part toxicological.

TABLE 5.—Combined effects of reduced oxygen and petroleum toxicity on juvenile American shad, *Alosa sapidissima*, experiments 1–2.

Petroleum product	Concentration (mg/l)	Dissolved oxygen (ppm)	Minutes elapsed	
			50% mortality	Total mortality
Gasoline	68	2.6–3.2	50	60
Diesel fuel oil	84	1.9–3.1	270	300

Diesel fuel oil, and especially gasoline, seemed to lose some of their toxic properties before the conclusion of a test. The 24- and 48-hour TL_m derived from the gasoline experiments were the same. Roberts (1926: 271–3) found that on exposure to air, extracts of gas oil and diesel oil lost much of their toxicity and attributed this to a possible loss of toxic volatile substances or to the oxidation of the toxic substances. Determining the chemical nature of the various petroleum products, although not attempted in the present study, evidently is important in the evaluation of their effect.

A synergistic relation appears to exist between the combined effects of low oxygen and oil pollution that increases their toxicity to fish. Oil concentrations that are tolerable to fish when accompanied by high oxygen levels probably become lethal when oxygen is just adequate for fish survival. As pointed out by Beak (1958:567–70), it has been demonstrated experimentally by various workers that the lethality of certain toxic substances is increased by accompany-

ing low dissolved oxygen conditions. In the case of oil pollution, low oxygen may be directly due to the oil pollutant. A surface oil layer retards air-water exchange of oxygen, and it is known that crude oils absorb this gas (Roberts, 1926:253). Doudoroff (1957:413) reported that high temperatures, extremes of pH, high concentrations of free CO_2, and certain other toxic substances can greatly increase the susceptibility of fish to low dissolved oxygen in natural waters.

Conclusions

1. Experiments were conducted on juvenile shad to indicate tolerance to reduced oxygen, toxicity of petroleum products, and the effect of reduced oxygen on toxicity of petroleum products.

2. Each test consisted of 10 shad in 30 gallons of water. In the reduced oxygen tests, oxygen was lowered by the test fish at different rates in open and covered aquaria or was maintained at desired levels by artificial aeration. In petroleum product bio-assays, water in each aquarium was circulated to permeate the pollutant added to the surface. Experiments on combined effect of reduced oxygen and petroleum products were conducted in the same manner as the above, and desired low levels of oxygen were maintained by addition of nitrogen.

3. Fifty percent mortality resulted at an oxygen concentration of 0.9 ppm when initial oxygen was reduced at a rate of 1.0 ppm per 9½ and 11 hours and at 1.4 ppm when oxygen was reduced at a rate of 1.0 ppm per 3 hours. No deaths occurred when dissolved oxygen was maintained between 1.8 and 3.8 ppm for 96 hours.

4. The 48-hour TL_m (median tolerance limit) values determined in the evaluation of toxicity of petroleum products to juvenile shad were 91 mg/l gasoline, 167 mg/l diesel fuel oil, and 2,417 mg/l bunker oil.

5. Petroleum product concentrations that were tolerable to juvenile shad when accompanied by dissolved oxygen greater than 6.0 ppm were lethal at oxygen levels ranging from 1.9 to 3.2 ppm.

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Bureau of Commercial Fisheries
Biological Laboratory
Beaufort, North Carolina

/ATER, BASIC ELEMENT *of marine research, envelops the U. S. Biological Lab-ratory, Beaufort, North Carolina. At the right center are the buildings of Duke Marine Laboratory, and, at the left, the town of Beaufort. Across the skyline uns Shackleford Banks, one of a series of thin islands which protect the coast f North Carolina from the open Atlantic. (U. S. Bureau of Commercial Fisheries)*

At Hatteras' Back Door

By G. B. TALBOT
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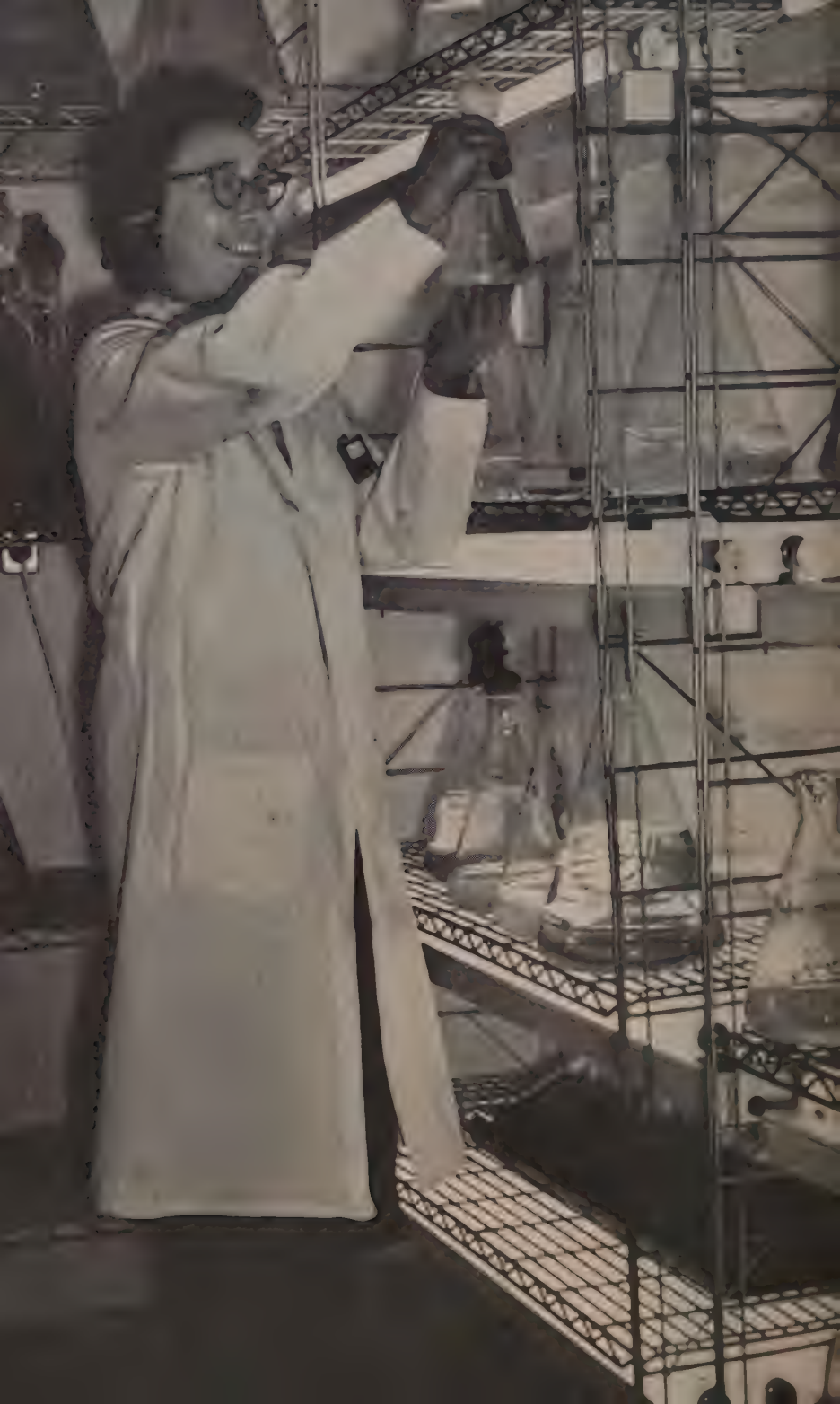
WHEN SIR WALTER RALEIGH'S expedition reached the shores of North Carolina in 1584, its adventurers were chiefly interested in finding gold or other precious objects. Abundant sea food was duly noted, however, and was a determining factor in establishing a colony in "Virginia," as the area was then called. The first colonists arrived in 1585, others in 1587, and settled on Roanoke Island, at the northern end of Pamlico Sound. Marine life formed a staple part of their diet.

"Lost Colony"

However, a supply ship from England, in 1590, could not locate the



onists and to this day they have en referred to as the "Lost Col- y." Nevertheless, recent studies in- ate that the Roanoke settlers may t have vanished completely, but rhaps relocated on Cedar Island out seventy miles to the south.

Although the mystery of the "Lost lony" has never been solved, and e discovery of valuable minerals l not materialize, the abundance marine life in this area continues, d it played a dominant role in the tlement of tidewater North Car- na.

Varied Marine Areas

T. N. Gill and William Stimpson ere the first scientists of note to cognize this area as suitable for arine research. Near Beaufort, hich these zoologists visited in 1860, e large tidal estuaries; several rivers d creeks; extensive sounds of salt, ackish, and fresh water; marshes; press swamps; large offshore banks, well as the ocean shore, with its pansive sandy beaches and broad ne areas.

In 1871-72, Elliot Coues and H. Yarrow, zoologists, visited Beau- rt and further stimulated interest the locality. They were followed the next few years by professors d students from Johns Hopkins University, who maintained a small laboratory in Beaufort for about ten years.

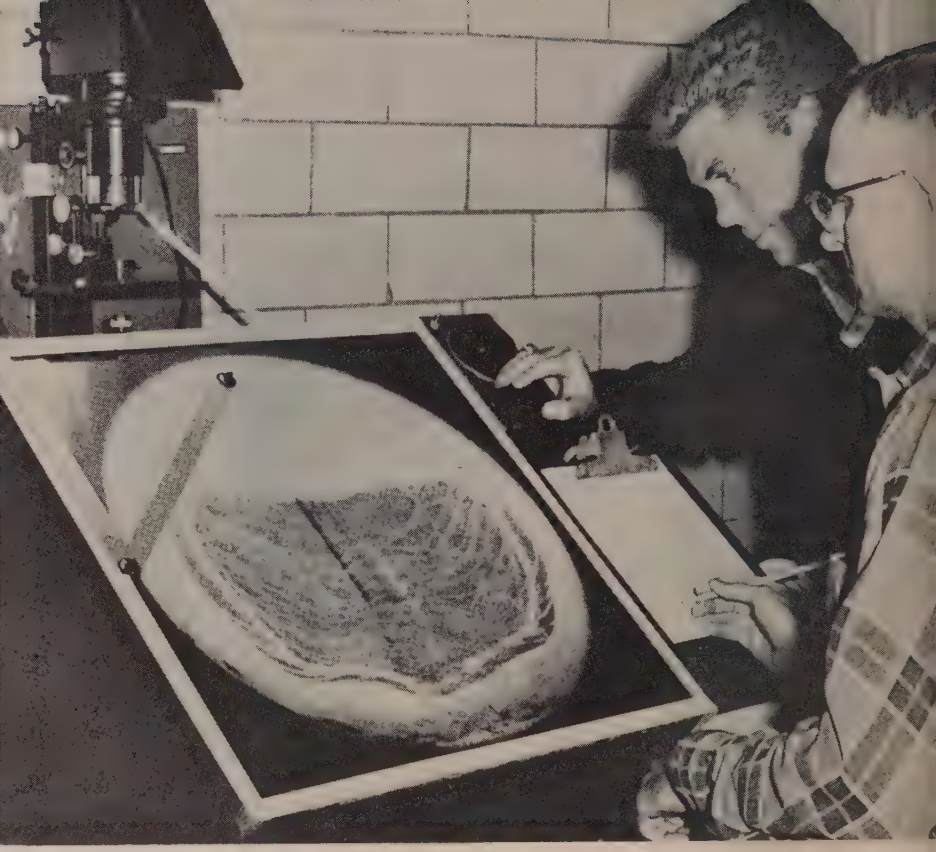
Cutting Red Tape

An act of Congress, approved May 12, 1900, authorized the U. S. Fish Commission to establish a biological station and laboratory in North Carolina. Through some oversight, however, funds were not provided for the purchase of land. At the suggestion of Professor I. A. Holmes, state geologist of North Carolina, this was not allowed to delay construction. About $400 was subscribed by several institutions—the University of North Carolina, the University of Virginia, Johns Hopkins University, South Carolina College and the University of Georgia for the purchase of a site. After careful investigation, Pivers Island, in Beaufort Harbor, was chosen. Work was begun immediately and a research laboratory and other buildings were completed in 1901.

Interrupted Only By Wars

Since that time marine research has been carried out by the Bureau of Commercial Fisheries at this station, known as the U. S. Biological Laboratory, except for brief interruptions during the two World Wars. Many of the most prominent biologists of our time have been associated with it. These include, among others, Brooks, Hildebrand, Grave, Wilson, Hopkins, Radcliff, Pearse, Mast, Hoyt and Hay. Their work laid a firm foundation upon which modern researchers can build.

PERATURE AND LIGHT *are controlled e room where the uptake of radio- e nutrients are determined. Here t is being made on marine plank- algae grown in enriched sea water. rescent bulbs simulate daylight, e a refrigerating unit maintains a tant 68°F. (U. S. Bureau of Com- cial Fisheries)*



AMERICAN SHAD SCALE, *enlarged 27½ times, reveals such secrets as age, number of times spawned, and age at first spawning. This specimen was obtained from the Connecticut River. (U. S. Bureau of Commercial Fisheries)*

Duke University established a marine laboratory adjacent to the Federal Station in 1938, and in 1947 the University of North Carolina founded the Institute of Fisheries Research in nearby Morehead City. The facilities of the three laboratories make this area an outstanding center for marine research.

In 1949 the Bureau of Commercial Fisheries began to modernize the station which had served so well fo half a century. A new fishery labora tory to replace the 1901 wooder structure, a radiobiological labora tory, a dormitory, a maintenanc building, a residence for the director and concrete road and parking are have now been completed.

The new fishery laboratory, servic building, dormitory, and residenc are of masonry construction, well suited to the Beaufort climate. Th laboratory is a one-story building 168 feet long by 32 feet wide.

A wing, 72 feet long and 32 fee wide, extends from the library at th

nter of the building. This contains lditional offices for the biological aff and allows full use of facilities y all staff members.

Protection from Radiation

The radiobiological laboratory is a ne-story frame building, 77 feet long y 44 feet wide, with an adjoining ing. The building is divided into veral laboratory rooms, containing ecial equipment for the various re-earch in progress. Frame partitions eparate the laboratory rooms, ex-ept where protection of instruments nd workers from penetrating radia-on is necessary. In these cases, 17-ch concrete walls extend from floor ceiling.

Other research facilities at the U.S. iological Laboratory include nine oval concrete pools supplied with salt and fresh water, each measuring approximately 96 square feet; two large concrete pools, approximately 30 by 40 feet, supplied with running sea water; a 30 by 40 foot fresh water pool; and a 30 by 80 foot tidal pen. These pools provide space for holding aquatic animals.

Laboratory Fleet

Two motor vessels are maintained at the station: a 40-foot cruiser equipped with a marine radio, galley and bunks for two; and a 26-foot V-bot-

TEDIOUS BUT NECESSARY FIELD WORK. *Raising the drag used to determine speed and direction of currents in the Newport River estuary. Such hydrographic studies help to determine causes for fluctuations in the abundance of blue crab populations. (U. S. Bureau of Commercial Fisheries)*

tom launch for daytime use. Outboard motor boats and trailers are also used.

Fishery research depends upon the needs of the commercial fisheries and special qualifications of the staff. At present, five major investigations are under way.

Research on American shad *(Alosa sapidissima)* of the Atlantic coast has been conducted since 1950 to determine the cause of the decline in abundance of this species, and to determine methods of stabilizing and increasing the yield. This can be done when the catch in a river, and the amount of gear used in making the catch each year, is known over a period of years.

Predicting Shad Runs

In the Hudson and Connecticut Rivers, where such data have been obtained, it was found that the number of fish allowed to spawn each year is the major factor in determining the size of shad runs. Mathematical equations now predict one year in advance the shad population that will enter the rivers. Fishing pressure can be regulated to allow the optimum number of spawners to produce maximum yields. In other words, it is now possible scientifically to manage these fish populations.

CRAB FLOATS, LINED WITH NYLON, *provide a means of checking the development of eggs of the yellowfin menhaden* (Brevoortia smithi). *Eggs and sperm are first obtained from ripe fish. The fertilized eggs are then placed in the floats, and fish are reared from eggs through larval stages. Specimens of these stages allow comparison and identification with plankton material taken from nets. (U. S. Bureau of Commercial Fisheries)*

Many facts concerning the life history of American shad were revealed during the study. Among these are the age of the fish, as well as the number of times it has previously spawned, by a method using scales from the fish. Perhaps the most interesting result, however, is the disclosure of the annual migration pattern of the species, involving a journey of over a thousand miles to the Gulf of Maine in the summer and back to the middle Atlantic region in the fall. This migration is made by immature as well as adult shad.

Crabs and Menhadens

Causes for the great fluctuations in abundance of blue crabs *(Callinectes sapidus)* are being sought at the laboratory. Research is concentrated in the south Atlantic States at present, but will be expanded into Chesapeake Bay when finances and adequate staff permit.

A third study involves Atlantic coast menhadens. Menhadens rank first *in volume* among all commercially caught fishes in the United States. Although not utilized as human food, menhaden are processed into meal, solubles and oil. While production is high at the present time, fluctuations in catches have occurred. The program will determine causes for these fluctuations, and the extent to which they are predictable.

Juveniles in Estuaries

Menhaden spawn at sea, but the eggs and larvae are carried into estuaries where the young may remain for periods up to a year before returning to the ocean. Studies to date have shown that along the Atlantic Coast of the United States the Atlantic menhaden *(Brevoortia tyrannus)* is the major species of commercial importance. The yellow-fin menhaden *(B. smithi)* is the principal species south of Cape Canaveral, Florida, while a third species in Florida, similar or identical to *B. Patronus* of the Gulf of Mexico, is found in lesser abundance.

A study of the juveniles in the estuaries has shown the existence of at least two subpopulations of Atlantic menhaden—one occurring north of Long Island and another south of Long Island. Apparently, however, the two groups mix when they enter the ocean.

An age analysis has disclosed that while most menhaden are caught during the first three years of their lives, some are caught up to the age of ten years. Certain brood years of fish have been found to be extremely abundant and sustain the fishery for several years. It is hoped that research will disclose the cause or causes responsible for the great abundance of young produced in certain years. Trends in the catches of menhaden will be followed for several years. With this information and the biological data it is possible that menhaden populations and catches will be predictable in future years.

Fish of Many Names

Atlantic coast striped bass *(Roccus saxatilis)* are known by several names. In New England they are called "strip-ped bass" or more commonly just plain "bass," since to an avid

SEINING FOR YOUNG ATLANTIC MENHADEN. *Although it is not a food fish for man the menhaden is a valuable food supplement for animals, and is one of the most abundant fishes in U. S. waters. Its early development, however, is dependent upon suitable conditions in bays, rivers, and estuaries. Hence such sampling by biologists shown here. (U. S. Bureau of Commercial Fisheries)*

striped bass sport fisherman there is only *one* bass. In Chesapeake Bay they are usually referred to as "rock" and elsewhere as "stripers" or "rock-fish." This species is eagerly sought by both commercial and sport fishermen. Aim of research here is to maintain the present adequate supply of fish for both groups by proper conservation measures.

Striped bass up to 125 pounds have been caught and 50 to 60 pounders are not uncommon, but fish less than six pounds in weight constitute almost the entire commercial catch along the Atlantic coast. These fish usually confine themselves to specific sounds, bays, and rivers, although they may overflow from these areas to the New England coast. Recent tagging experiments show that six to fifty-pound "jumbo" stripers, found during the winter off the North Carolina coast annually migrate into Chesapeake Bay in the spring and to New England waters in the summer.

More Water For Fish!

Research on North Carolina striped bass and on various aspects of its life history by the laboratory staff is playing a part in the licensing of a new power dam on the Roanoke River. This is expected to result in more waters for striped bass spawning there and helps to put the water demand of a spawning fish population on a par with those of industry.

One of the most important research projects is a joint effort of the Atomic Energy Commission and the Bureau of Commercial Fisheries to study the accumulation of radioisotopes by marine phytoplankton, invertebrates, and various species of fish. A radioisotope coming into contact with sea water will either go into solution or form particles. Which of these occurs to a particular radioisotope in atomic wastes will determine whether or not it enters into the metabolism of marine organisms. Many radioisotopes form particles that cannot be broken down in the digestive tract of animals. Thus they cannot pass through the lining of the digestive tract and enter into the metabolism of the organism.

How a Fish Becomes Radioactive

Concentrators of food elements, the microscopic plants or phytoplankton that drift in the upper layers of the water, accumulate most radioisotopes, and thus play an important role in passing them to marine animals. A large variety of animals feed on phytoplankton, including animal plankton (zooplankton), oysters and related animals, and some species of fish. These animals have straining devices which they use to filter the phytoplankton from large volumes of water.

Radioisotopes contained in the phytoplankton when eaten may enter into the life chemistry of these animals and be concentrated to considerably high levels in their bodies. The zooplankton are large enough to be eaten by young fish, and in some instances by adult fish, and may be a means by which certain radioisotopes enter the body of fish.

Radioactive Danger

All radioisotopes, however, do not necessarily pass through a number of smaller animals before reaching large fish. Some radioisotopes can be taken directly from the water by an animal anywhere within the food-web. Since elements within a plant or animal are in a dynamic state, continually entering and leaving, a radioactive plant or animal will eventually lose most of its radioactivity if kept in non-radioactive sea water.

This investigation provides data necessary for proper waste disposal practices, and for the safe operation of nuclear-powered ships in coastal areas. The information is also valuable in the development of monitoring programs, designed to detect and evaluate hazards from normal or accidental pollution of inshore waters and marine resources by radioactive materials.

State Cooperation Important

In addition to research activities, the Branch of Statistics of the Bureau of Commercial Fisheries maintains offices at the laboratory. Fisheries statistics on catch, gear, boats, and fishermen are compiled for North Carolina, South Carolina, and Georgia, with the cooperation of state agencies. Since management research depends upon fishery statistics, this service is of considerable help to most of the research projects undertaken at the laboratory.

During recent years the value of

North Carolina's fishery resources alone has exceeded eight million dollars per year. Fishery products along the whole Atlantic and Gulf coasts amount to over three million tons, valued at $225 million annually. Thus, it can be seen that while Sir Walter Raleigh and his colonists hoped for gold, their early efforts led to the discovery of a much greater and more valuable resource in the fisheries.

Furthermore, this is a renewable resource which, if properly conserved, can continue to produce annually, rather than being exhausted as in the case of mineral deposits. It is the function of the U. S. Biological Laboratory, as part of the Bureau of Commercial Fisheries working with state and other conservation agencies, to help the fishing industry by giving, among other things, assistance in research and resource management to assure sustained production of this most valuable national resource.

TAGS REVEAL FISH *wanderings. Tagging a "jumbo" striped bass along the Nort Carolina coast is a two-man job, and little wonder when this specimen tipped th scales at 47 pounds and was over 42 inches long. Tag returns have shown tha these large fish winter along the North Carolina coast, spawn predominately i Chesapeake Bay streams, then migrate northward, spending the summer o Massachusetts and Rhode Island. (U. S. Bureau of Commercial Fisheries)*

Hermaphroditic Skipjack

Richard N. Uchida

Reprinted from PACIFIC SCIENCE
April, 1961

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Hermaphroditic Skipjack[1]

RICHARD N. UCHIDA[2]

TWO PAIRS of skipjack (*Katsuwonus pelamis*) gonads, each having male and female components, have come to my attention in the past 3 years. The first was received from Mr. Thomas S. Higa, proprietor of a Honolulu fish retail market, in April 1957. Mr. Higa recovered the gonads from a neighboring fish retailer who had discovered them in a freshly eviscerated 16-lb. skipjack. This fish was captured by the "Orion," a commercial skipjack vessel, on April 11, 1957, off Makua, Oahu, from a school of 15- to 18-lb. skipjack.

The ovo-testes (Fig. 1) were typically paired and elongate, joined posteriorly, and weighed 121 gm. (fresh weight). The male and female components were easily discernible. The left gonad was divided into three segments; the anterior one-sixth and posterior one-third were ovarian and the remainder testicular. The right gonad was divided into two segments; about two-thirds of the anterior portion was testicular and the remainder ovarian. Figure 2 shows the length of each of these segments.

The cream-colored testicular sections were solid and somewhat flattened in cross-section, and did not seem to be atypical in any way. There was no running milt present, but their size suggested that they were in a rather advanced stage of maturity. All ovarian sections were pinkish, but differed in firmness. The posterior segments were hollow and flabby, with a ribbed internal cavity extending their entire length. The single anterior ovarian section was nearly round in cross-section and rather turgid.

Detailed examination of the ovo-testes was made after they had been preserved in 10 per cent formalin. The longitudinal duct of each testicular section could be followed posteriorly to the juncture of the testicular and ovarian segments, after which the ductus deferens became obscured in the network of blood vessels on the surface of the ovarian section. No openings of the ductus deferens were detected anywhere in the area of the urogenital sinus.

The two posterior ovarian sections were joined posteriorly by a single oviduct which opened into the urogenital orifice. No duct could be found in the single anterior ovarian segment.

Microscopic examination of the ova was made to determine their degree of maturity. The lumen of the anterior ovarian section was filled

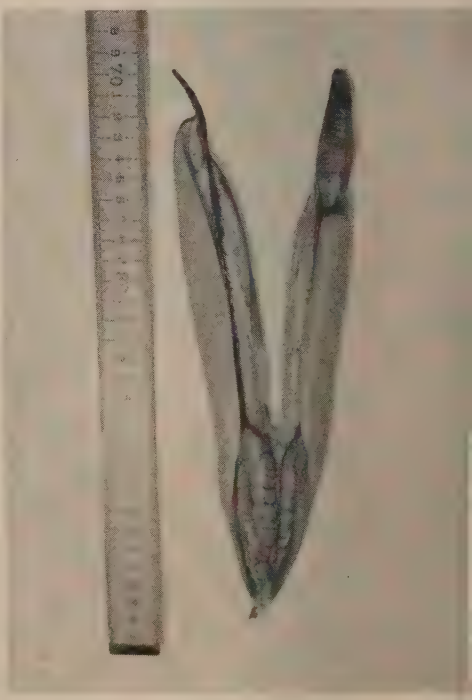

FIG. 1. The ovo-testes of a hermaphroditic skipjac (ventral view).

[1] Published with permission of the Director, U. S. Bureau of Commercial Fisheries. Manuscript received July 29, 1960.

[2] Fishery Research Biologist, Honolulu Biological Laboratory, U. S. Bureau of Commercial Fisheries, Honolulu, Hawaii.

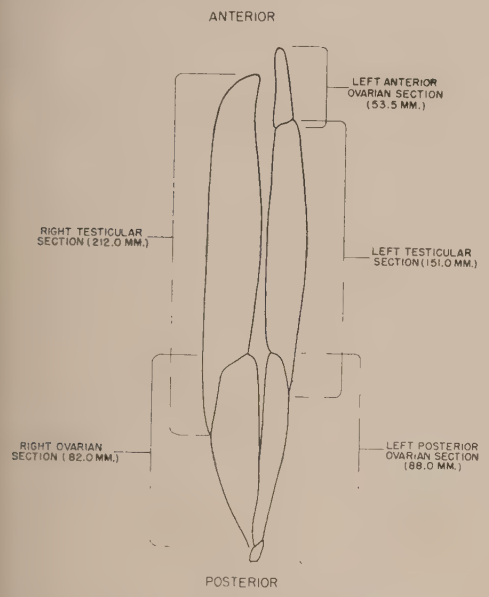

FIG. 2. Outline of the ovo-testes, showing the location and size of the male and female components (ventral view).

with a compact mass of resorbing ova, while the peripheral portion contained ova ranging from small, transparent stages to larger, opaque ova. The average diameter of 25 randomly selected larger, opaque ova was 0.504 mm. The posterior ovarian sections contained similar small and large ova, but no resorbing ova were present. Average diameters of randomly selected ova from these parts were 0.543 mm. for the left posterior member and 0.514 mm. for the right.

The presence of residual ova in the anterior section suggests that the fish had been a functional female. Assuming that the ova in each of the ovarian sections ripened at the same time, it is possible that ova were extruded from the posterior sections at spawning time, whereas ova in the anterior section could not be extruded because of the lack of an adequate duct. This could account for the presence of the resorbing ova in the lumen of the anterior ovarian section. Since the testicular sections were well developed and constituted a large part of the gonads, the fish may also have been a functional male.

The discovery of the second pair of ovo-testes was reported to the Honolulu Biological Laboratory on March 10, 1960, by Mr. Richard Nakashima of Honolulu, who found them in a 10-lb. skipjack.

The gonads, outlined in Figure 3 and labeled *A* and *B* for purpose of identification, were not joined posteriorly as a result of mutilation to both posterior ends during removal, and, therefore, could not be identified as to position (left or right). Both gonads were distinctly separated into three parts; an anterior ovarian section, a middle testicular portion, and a torn, fragmentary ovarian segment posteriorly. The testicular segments were similar to those found in the ovo-testes previously described, and contained no running milt. The ovarian sections were predominantly yellow with a tinge of pink. The anterior segments were flabby and hollow.

A starch suspension colored with powdered carmine was injected into the posterior ovarian section of gonad *A* and the flow of injected material indicated the presence of a duct connecting the two ovarian parts. A similar injection was attempted with gonad *B*, but failed

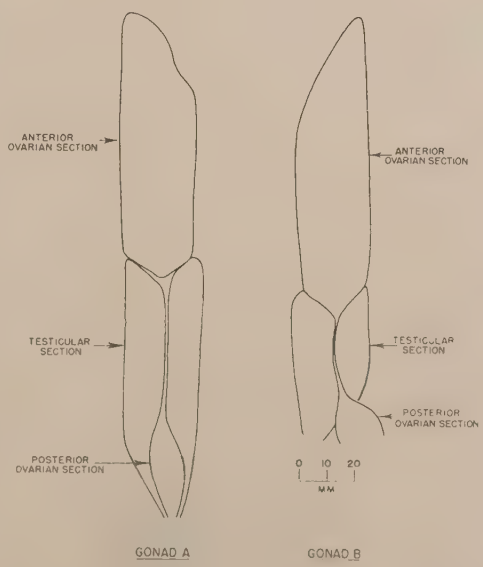

FIG. 3. Outline of the ovo-testes, showing the location and relative size of the male and female components.

to reveal any ducts owing to excessive tissue damage.

Ova diameter measurements revealed that the posterior ovarian section of gonad *A* and both ovarian segments of gonad *B* were identical in their degree of development. The ova ranged from small, primitive ova to larger, opaque ova. Average diameters of 25 randomly selected ova of the most advanced group were 0.479 mm. for the posterior ovarian section of gonad *A* and 0.476 mm. and 0.479 mm. for the anterior and posterior ovarian sections, respectively, of gonad *B*.

The development of the anterior ovarian section of gonad *A* was dissimilar to any of the sections previously examined. Its lumen contained a loose mass of large, ripe, resorbing ova, together with a few completely degenerated ova. The peripheral portion of the section contained only primitive ova. Those intermediate to the primitive and the large, resorbing ova were absent.

The presence of residual ova indicates that this fish also had been a functional female. Again, it is not clear whether the ova remnants were the unexpelled portions of a previous successful spawning or a group of ripe ova that were not expelled owing to the inadequacy of the duct. Damage to the posterior portions of both gonads made it impossible to determine whether the male ducts were connected to the exterior, but since the testicular segments were well developed, this fish may also have been a functional male.

Hermaphroditism in skipjack is an extremely rare occurrence. So far as is known, only one other example has been recorded and described (Nakamura, H., 1935, Trans. Nat. Hist. Soc. Formosa 25(141): 197–198; in Japanese).

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THE EFFECT OF TEMPERATURE ON THE GROWTH AND SURVIVAL OF SEVERAL MARINE ALGAL SPECIES

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The importance of temperature as an ecological factor limiting the distribution of species is well known. Protozoa and algal species have been found in extreme temperature ranges and have been considered among the most resistant of all organisms. Flagellates have been found living in hot springs at 51° C., algal species at 70° C. to 80° C. and even as high as 90° C. (Davenport, 1897). These examples are interesting, but exceptional, and active stages of "protists" are usually killed as the temperature approaches 45° C. (Hall, 1953). Although information is available on the general characteristics of the biothermal range for many organisms, specific information on the temperature tolerance of individual species frequently is lacking. Such information as is available has often been obtained from nature where the temperature of the natural habitat is subject to fluctuations and, hence, observations may be unreliable (Spector, 1956). Information gained from laboratory studies under defined conditions is an aid in the interpretation of ecological data, just as ecological data may guide laboratory experimentation.

From a practical point of view, interest in the culture of algal and protozoan organisms as food sources for metazoan forms (Gibor, 1956; Davis and Guillard, 1958; Provasoli *et al.*, 1959) makes it desirable to accumulate detailed information on the factors necessary for the survival and growth of particular organisms *in vitro* and *in vivo*. Studies on the temperature characteristics of plankton species are a prerequisite to proposed studies on the temperature tolerance of bivalves (Davis, personal communication). The following is a report of an investigation into the biothermal range of several species of marine plankton organisms that are of importance to filter-feeding animals.

Material and Methods

Temperature requirements of representatives of three classes of phytoplankters were investigated.[1] *Monochrysis lutheri* and *Isochrysis galbana* of the class Chrysophyceae were used, as was *Phaeodactylum tricornutum*, also considered a chrysophyte by Hendey (1954), but which has been used by several workers as *Nitzschia closterium* (Ehrenberg), Wm. Smith forma *minutissima*, (Allen and Nelson, 1910). Lewin (1958) gives the most recent discussion of the taxonomy of *Phaeodactylum tricornutum* and considers it a chrysophyte of the order Bacillariales and proposes a new suborder with *P. tricornutum* as the only known species. Representatives of the class Chlorophyceae included *Dunaliella euchlora*,

[1] The organisms used were in bacteria-free culture, and were from the same cultures used by Davis and Guillard (1958). Source data are, therefore, not repeated here.

Platymonas sp., *Chlamydomonas* sp. of the order Volvocales; *Chlorococcum* sp., *Chlorella* sp. of the order Chlorococcales; and *Protococcus* of the order Chaetophorales. Temperature requirements of the pennate diatoms, *Nitzschia laevis, Amphiprora* sp. and *Amphora* sp., and of the centralean diatom, *Actinocyclus* sp., were also investigated.

Glass-covered, 25-milliliter Fernbach flasks were used as culture vessels. These flasks allow for complete illumination and an adequate surface-volume relationship. Each vessel contained 10 ml. of medium and was inoculated with 0.5 ml. of a bacteria-free unialgal stock culture. Stock cultures from which the inocula were made are maintained at 20.5° C. ± 1° C. in a light room. The basal medium consisted of the following: KH_2PO_4, 20 mg.; thiamine HCl, 0.4 mg.; biotin, 2 μg.; vitamin B-12, 2 μg.; $NaNO_3$, 150 mg.; ferric sequestrene (13% Fe), 10 mg.;

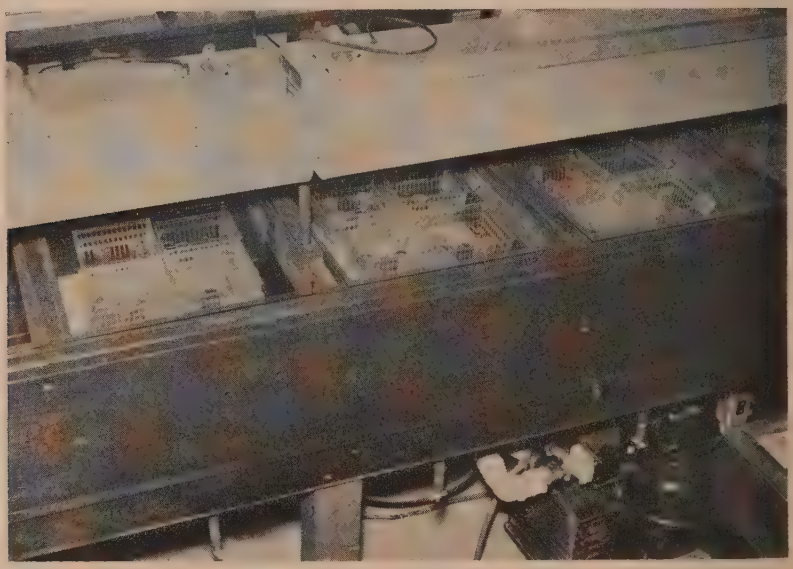

FIGURE 1. Constant temperature apparatus, showing four of the six individual baths, the refrigerating system, the lighting system and the culture vessels.

NH_4Cl, 50 mg.; $CuSO_4 \cdot 5H_2O$, 0.019 mg.; $ZnSO_4 \cdot 7H_2O$, 0.044 mg.; $CoCl_2 \cdot 6H_2O$, 0.022 mg.; $MnCl_2 \cdot 4H_2O$, 0.360 mg.; $Na_2MoO_4 \cdot 2H_2O$, 0.0126 mg.; sea water, 1 liter (22 to 27 ppt). NH_4Cl was eliminated from the basal medium for *I. galbana*.

Experimental temperatures were maintained in a series of constant temperature baths regulated to ± 0.5° C. The culture flasks were submerged on plastic mesh racks into the water baths and incubated at temperatures ranging from 8° C. to 39° C. The apparatus allows for the determination of the effects of six temperatures simultaneously. Light was received from a bank of cool fluorescent bulbs suspended over the water bath to give maximum illumination with a minimum amount of heat (Fig. 1). At periodic intervals cultures were observed for

multiplication of organisms. Where no growth occurred, tests for viable organisms were made by transferring a small inoculum to the basal medium, incubating at an optimum temperature and observing whether multiplication was resumed. In other experiments to determine the effect of temperature on the rate of growth and population density, cultures were incubated in loosely capped calibrated screw-cap test tubes, and growth measured as optical density in a Beckman Model DU Spectrophotometer with test tube adapter assembly.

Results

All of the organisms tested grow normally within the temperature range from 18° C. to 22° C., but there was considerable variation between species, in the minimum and maximum temperatures tolerated (Table I). The maximum temperature for normal growth of the three species of chrysophyte organisms in an eight-day incubation period was 24° C. to 27° C. A temperature of 27° C. resulted in poor growth of *P. tricornutum* and *M. lutheri* and no multiplication of *I. galbana*. At 29° C., *M. lutheri* and *P. tricornutum* also showed no growth. It appeared that *M. lutheri* and *P. tricornutum* cells incubated at 30° C. and *I. galbana* at 27° C. were no longer viable, since growth was not resumed when cultures were transferred to a temperature of 20.5° C. for eight days (Table II). However, with longer incubation periods (25 days) at a favorable temperature, *M. lutheri* cells from a culture that had been incubated at 30° C. did resume normal growth. Similarly, although cells of *I. galbana* incubated at 27.5° C. showed no growth after seven days at an optimum temperature, normal multiplication was resumed by the twenty-fifth day. However, cells incubated at 30° C. did not resume growth.

Table I

The growth response of plankton organisms at various temperatures (degrees centigrade)

	No growth	Growth less than control	Growth equal to control at 20.5° C.	Growth less than control	No growth
M. lutheri	8–9°	12°	14–25°	27°	29–35°
I. galbana	8–9°	12°	14–22°	24–25°	27–35°
P. tricornutum	—	—	8–24°	27°	29–35°
D. euchlora	8–9°	—	12–35°	—	39°
Platymonas sp. (#1)	—	8–9°	12–32°	—	35°
Chlamydomonas sp. (Y)	8–9°	—	14–28°	—	32–35°
Chlamydomonas sp. (11/35)	—	8–9°	14–27°	—	—
Chlorella sp. (#580)	8–9°	12°	14–35°	—	—
Chlorella sp. (UHMC)	8–9°	12°	14–29°	—	32–35°
Chlorococcum sp.	—	—	15–30°	—	—
Protococcus sp. (T3)	8–9°	—	12–25°	—	26–32°
Protococcus sp. (T9)	8–9°	—	12–32°	—	35°
Actinocyclus sp.	—	15–17°	18–27°	30°	—
Amphiprora sp.	—	—	8–30°	—	—
N. laevis	—	—	15–24°	27°	30°
Melosira sp.	8–9°	14°	15–24°	—	27–30°
Amphora sp.	—	—	8–30°	—	—

Microscopic observations indicated that *I. galbana* were most actively moving

TABLE II

Tests for viability at temperatures that inhibited growth. (+ = growth equal to that of controls, ± = growth less than controls, 0 = no growth)

	Initial incubation temperature ° C.	Growth after 7 days	Growth 7 days after transfer to 20.5° C.
Platymonas sp. (#1)	7.5	±	+
	35	0	±
Chlamydomonas sp. (11/35)	7.5	0	+
	35	0	+
D. euchlora	7.5	0	+
	39	0	0
Protococcus sp. (T9)	7.5	0	+
Protococcus sp. (T3)	7.5	0	+
	32	0	0
	39	0	0
Chlorella sp. (580)	7.5	0	+
Chlorella sp. (UHMC)	7.5	0	+
	32	0	0
M. lutheri	7.5	0	+
	30	0	0
	32	0	0
I. galbana	7.5	0	+
	27.5	0	0
	30	0	0
P. tricornutum	28	0	+
	30	0	0
	32	0	0
Melosira sp.	27	0	0
	30	0	0
N. laevis	30	0	±

at 15° C. At 24° C. to 25° C. organisms appeared sluggish and pale, and at 27° C. cells settled out of suspension and only an occasional complete motile cell was observed. *M. lutheri* appeared to be most active at 18° C.; at 27° C., cells seemed sluggish and at 30° C., most of the cells were fragmented and only an occasional complete motile cell was observed.

When subjected to a temperature of 39.5° C., *M. lutheri* and *I. galbana* lost motility within 10 minutes, whereas the only motile chlorophyte tested, *D. euchlora*, remained motile for 45 minutes. In observations made five days after return to a favorable temperature, it appeared as if the viability of *M. lutheri* was affected within 20 minutes and that of *I. galbana* and *P. tricornutum*, within 10 minutes

(Table III). However, observation 13 days after return to normal temperature showed that there was some growth in all *M. lutheri* cultures, even those exposed to 39.5° C. for 65 minutes, in *P. tricornutum* exposed for 35 minutes and in *I. galbana* for 15 minutes.

The Chlorophyceae, as a whole, were more resistant to elevated temperatures than the Chrysophyceae. Of the motile Chlorophyceae, *D. euchlora* was the most temperature-resistant, *Platymonas* sp., the next, and *Chlamydomonas* sp., the least resistant. *D. euchlora* cells, exposed to 39.5° C. for 65 minutes, resumed multiplication within a few days after return to 20.5° C. (Table III), although they showed no growth during the seven-day incubation period at 39° C. (Table II). One strain of *Protococcus* sp. (T9) seemed to be more temperature-resistant than another strain (T3). *Protococcus* sp. (T9) grew at 32° C. but strain (T3) was inhibited at 27° C. (Table I). *Chlorella* sp. (580), *Chlorococcum* sp. and *Protococcus* sp. (T9) were not affected by a 65-minute exposure to 39.5° C.

Growth of the diatoms, *Amphiprora* sp., *Amphora* sp. and *Actinocyclus* sp., was not appreciably affected by temperatures between 8° C. and 30° C., but *N. laevis* and *Melosira* sp. did not grow at 30° C.

Platymonas sp. and *Chlamydomonas* sp. (11/35), incubated for seven days at 35° C., and *N. laevis* incubated at 30° C., were capable of resuming growth when

TABLE III

Thermal inactivation and death times at 39.5° C. as shown by loss of motility and failure to resume growth when returned to 20.5° C. (+ = growth equal to that of controls, ± = growth but less than that of controls, 0 = no growth)

Minutes at 39.5° C.		*M. lutheri*	*I. galbana*	*D. euchlora*	*P. tricornutum*	*Chlorella* sp. (580)	*Chlorococcum* sp.	*Protococcus* sp. (T9)
0**	% motile	100	100	100	*	*	*	*
	growth†	+	+	+	+	+	+	+
5***	% motile	50	25	100	*	*	*	*
	growth†	+	+	+	+	+	+	+
15	% motile	0	0	100	*	*	*	*
	growth†	±	0	+	0	+	+	+
25	% motile	0	0	75	*	*	*	*
	growth†	0	0	+	0	+	+	+
35	% motile	0	0	5	*	*	*	*
	growth†	0	0	+	0	+	+	+
55	% motile	0	0	0	*	*	*	*
	growth†	0	0	±	0	+	+	+
65	% motile	0	0	0	*	*	*	*
	growth†	0	0	±	0	+	+	+

* Species non-motile.
** Controls-returned to 20.5° C. immediately.
*** Time required for cultures to reach 39.5° C.
† Determined 5 days after return to 20.5° C.

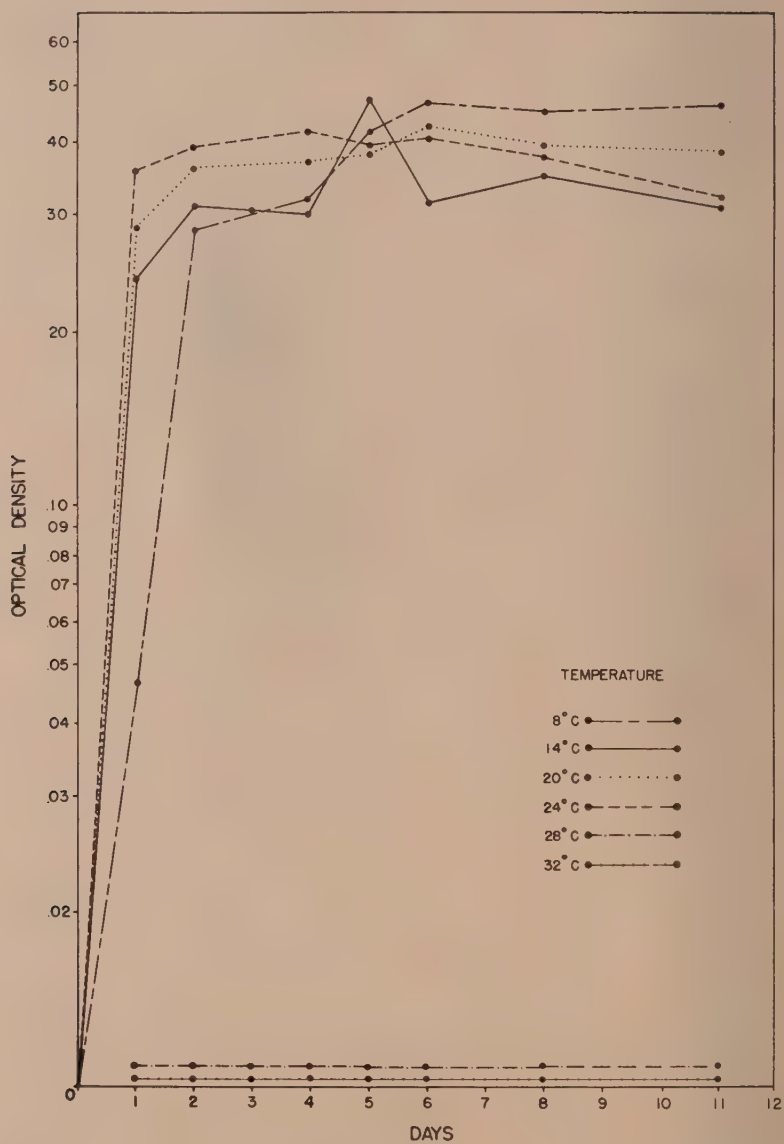

FIGURE 2. The effect of incubation temperatures of 8° C. to 32° C. on the growth of *Phaeodactylum tricornutum.*

transferred to 20.5° C. After a similar incubation period, *D. euchlora* at 39° C., *Protococcus* sp. (T3) at 32° C. to 39° C., *Chlorella* sp. (UHMC) at 32° C. and *Melosira* sp. at 30° C. were apparently not capable of resuming growth when transferred to 20.5° C. (Table II).

In every case in which growth of a species was inhibited by low temperature, growth was resumed when organisms were returned to 20.5° C. (Table II).

Quantitative measurements of the rate of growth and final population levels attained by *P. tricornutum* and *Chlorella* sp. (580) showed that *P. tricornutum* grew significantly faster at 14° C. than at 8° C. but that there was little difference in rates of growth at temperatures from 14° C. to 24° C. The maximum popula-

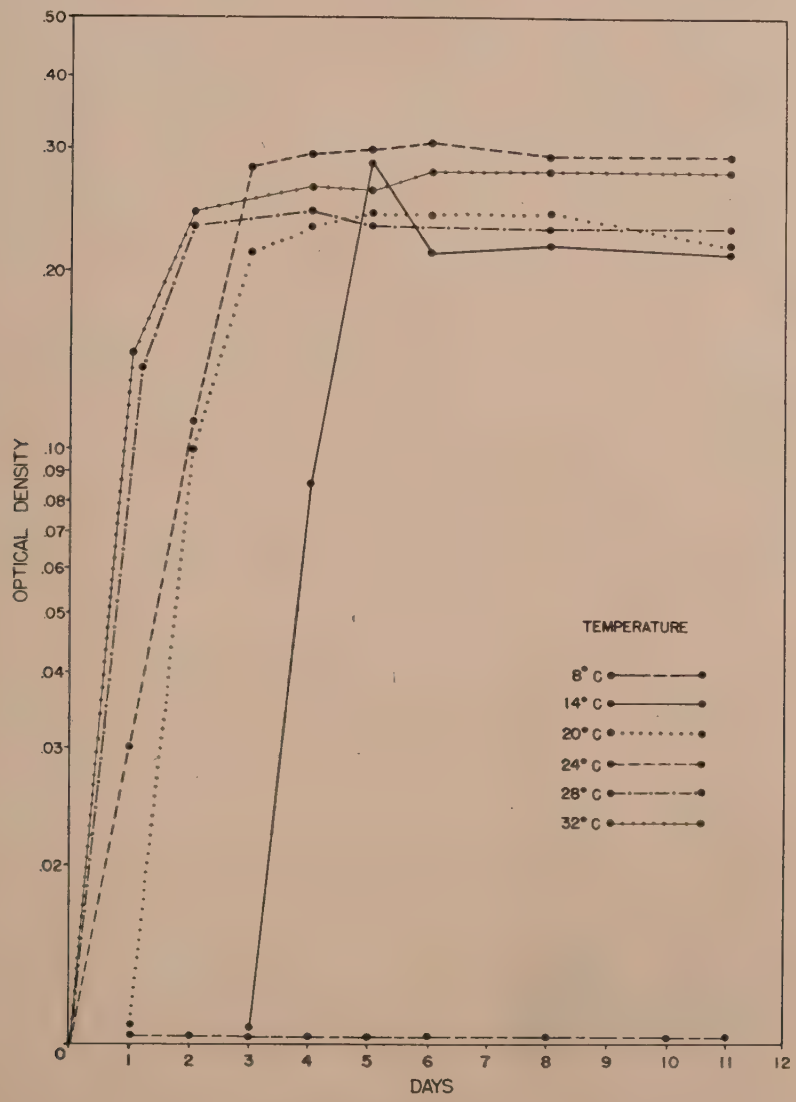

FIGURE 3. The effect of incubation temperatures of 8° C. to 32° C. on the growth of *Chlorella* sp. (580).

tion level attained, before growth leveled off, increased with each increase in temperature from 8° C. to 24° C., but no growth occurred at temperatures of 28° C. or 32° C. (Fig. 2). *Chlorella* sp. (580), conversely, showed no growth at 8° C. but grew rapidly at all temperatures from 14° C. to 32° C. At 14° C. and 20° C. initiation of growth appeared to be delayed and the maximum population level was achieved at 24° C. (Fig. 3).

Discussion

For the chrysophyte organisms tested the upper temperature limits for rapid growth appear to be relatively low, between 24° C. and 27° C. It has been reported that for *Prymnesium parvum,* also a chrysophyte, the upper temperature limit for three strains was 21° C. (Shilo and Aschner, 1953). It may be that this low temperature tolerance is a characteristic of the class. Droop (1953) isolated *M. lutheri* from pools with midday temperatures of 26° C. to 27° C. but, of course, this was not a continuous temperature. Our experiments show that a few individuals of an *M. lutheri* population are capable of surviving at 30° C. and multiply when returned to favorable temperature.

It was found that the maximum temperature for multiplication of *I. galbana* is about 2° lower than that for *M. lutheri* and that the latter species is also more temperature-resistant. In an eight-day incubation period, growth of *I. galbana* was poor at 24° C. and no growth occurred at 27° C. From visual observation, growth appeared to be best at 18° C. to 20° C. Kain and Fogg (1958) found that the optimum temperature for *I. galbana* was between 20° C. and 25° C. and, although they found that there was no growth at 30° C., exposure at this temperature was not lethal. In our experiments we found that cells incubated for eight days at 30° C. did not appear viable even when cells were transferred to an optimum temperature for a period of 25 days. The difference in results may stem from two sources. The English investigators used for their experiments a culture acclimated to an incubation temperature of 25° C., whereas our stock cultures are kept at 20.5° C. ± 1° C. In addition, these investigators used a natural sea water enriched with a soil extract as an incubating medium. The addition of particular crude factors may also alter the maximum tolerated temperature. Recent work has shown that temperature tolerance in the upper temperature regions for flagellates is variable, depending upon the nutritional components of the medium (Hutner *et al.,* 1957). The latter workers showed that, at an elevated temperature, there may be a rise in the requirements for particular vitamins, trace metals or crude factors.

Although the maximum temperature of a marine environment is considered 30° C. to 36° C. (Spector, 1956), the temperature of a particular area may reach higher values, since it is dependent on the absorption of light by an algal mass, or by the depth of a shallow tide pool. Survival of organisms in nature, where high temperatures may be reached, could also be dependent upon the organic content of the water and, thus, the work of Hutner *et al.* (1957) puts a new light on the interpretation of ecological data. Temperature data obtained in different laboratories must also take into consideration the nutritional milieux as well as the past history of the organism. It may be that organisms acclimated to elevated

temperatures will have a higher temperature resistance than other strains maintained at lower temperatures.

Time is also an important factor in determining the biothermal range for a "protist." The end point assay is subject to criticism, since it is dependent upon the survival of an individual organism and an analysis for this variant is being made. The temperature range for growth is narrower than that for survival.

Various theories have been proposed to account for the thermal death of an organism. These include an increase of internal protoplasmic viscosity, vacuolization of the protoplasm due to a release of calcium ion, denaturation of proteins or action on the lipid components of the cell (Heilbrunn, 1952), as well as a nutritional starvation (Hutner *et al.*, 1957). A clue to the nature of thermal death in these organisms may be furnished from studies on their suitability as foods for nutritionally-fastidious metazoan species. Loosanoff (1959) used a mixture of phytoplankton, consisting largely of *Chlorella* sp., to feed *Venus mercenaria* larvae at temperatures of 18° C. to 30° C. with satisfactory results. Experiments show that *Chlorella* sp. is not appreciably affected by a temperature of 30° C. However, in experiments using a mixture of *M. lutheri* and *I. galbana* as food, growth of larvae occurred only up to a temperature of 24° C.; at 27° C., growth was erratic (Davis, personal communication).

This inability of larvae to utilize these foods at temperatures above 27° C. may be due to the fragmentation, clumping and settling out of the food organisms. There is evidence to indicate that physical characteristics of plankton are significant in the utilization as food (Davis and Guillard, 1958). Another interesting possibility is that for the growth of bivalves there may be a nutritional factor or factors provided by the flagellates, that are heat-labile. Because the temperatures are similar, at which growth of larvae and growth of flagellates are inhibited, the possibility suggests itself that it is the heat inactivation of the same nutritional component that is the limiting factor for the growth of the flagellates as well.

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Records, Ages, and Growth of the Mooneye, *Hiodon tergisus*, of the Great Lakes

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Records, Ages, and Growth of the Mooneye, *Hiodon tergisus*, of the Great Lakes

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ABSTRACT

Mooneyes (*Hiodon tergisus*) are very scarce in the upper three Great Lakes since only four specimens have been received from Lake Michigan, one from Lake Huron, and none from Lake Superior. The published statistics of the mooneyes are erroneous. Those of 1931 of Lake Michigan were perhaps chubs (*Coregonus* spp.) and those of Lake Huron of 1929 were also chubs and of 1934, 1949, and 1951 were gizzard shad (*Dorosoma cepedianum*) but since 1956 were alewives (*Alosa pseudoharengus*). Mooneyes are common in Lakes Erie and Ontario and perhaps in Lake St. Clair but are commercialized only in the States of Ohio and Michigan. Virtually all Lake Erie mooneyes were caught in trap nets, pound nets, and seines in less than 35 feet of water. Their life-history data collected in 1927-31 included lengths and weights of age-groups I–VII, calculated increments and lengths based on both anterior radii and lateral diameters of scales, length–weight relationships, and sexual maturity. Apparently mature specimens exceeded 8.8 inches, 3.25 ounces, and age-group I.

On September 12, 1943, a female mooneye (*Hiodon tergisus*) was received from Cyril A. Nelson, a Michigan conservation officer. Al Thompson, a commercial fisherman of Rogers City, Michigan, had caught the specimen in a 6-foot shallow trap net which had been set in 12 feet of water one-half mile from the range lights of Presque Isle Harbor, Lake Huron. The mature mooneye measured 14 inches total length, weighed 14.2 ounces, hatched in 1935, and belonged to age-group VIII. It has been deposited in the Museum of Zoology, University of Michigan (Cat. No. 177274). So far as is known, this mooneye is the first one and the only one taken from Lake Huron.

Radforth (1944) recorded on a map mooneyes in western Lake Superior, Georgian Bay, and off the northern point of Bruce Peninsula in Lake Huron proper (an error was made in the legend of the figure: actually No. 2 locates mooneyes, No. 3 goldeyes). The author reported that the details of the total distributions of these two species had been dealt with by Kerswill[1] and several new records had extended the range of the goldeye (*Hiodon alosoides*).

At my request Dr. J. R. Dymond examined Kerswill's manuscript and found no occurrence of the mooneye in Lakes Huron and Superior. He also consulted John Budd, who stated that no one of his staff had ever taken or seen a mooneye in South Bay, Manitoulin Island, or in Georgian Bay. Neither the literature listed by Radforth nor Van Oosten's (1957) extensive bibliography of the Great Lakes publications revealed any record of a mooneye in Lakes Huron and Superior. If Radforth had seen the records or specimens of mooneyes from these lakes she should have referred to the sources of information.

The published statistics of the mooneye of the Great Lakes or of the gizzard shad (*Dorosoma cepedianum*) and alewives (*Alosa pseudoharengus*) are not always reliable. It is well known that many commercial and sport fishermen used the name "mooneye" not only for the real mooneyes but also for the gizzard shad and alewives because all three species are similar in general appearance, having a silver-colored and slab-sided body with a narrow belly.

Years ago, and probably even now, certain chubs (ciscoes) were also called "mooneyes" because they had comparatively large eyes, especially the kiyis (*Coregonus kiyi*). The 1931 United States record of 6,105 pounds of mooneyes caught in gill nets from the Wisconsin waters of Lake Michigan, although mooneyes had never been listed in the statistics of Lake Michigan in any other year, may be in error. Later it will be shown that mooneyes have seldom been caught in gill nets and at depths below 35 feet where most of the Lake Michigan gill nets have been operated.

Genuine mooneyes inhabit Lake Michigan but apparently are rather scarce. The few valid records actually revealed wide distribu-

[1] Kerswill, J. C. (1937) A taxonomic and distributional study of *Amphiodon alosoides* and *Hiodon tergisus*. M.A. Thesis, University of Western Ontario.

tion of the species. The first specimen, an adult 214 millimeters standard length, was submitted for identification on June 1, 1922, by Smith Brothers, Port Washington, Wisconsin. The details of the other specimens are as follows: September 17, 1938, from a pound net at Gladstone, Michigan, sent by Roy Jensen; July 6, 1941, from a pound net at Saugatuck, Michigan, an adult 253 millimeters standard length, sent by Frank Sewers; January 31, 1944, from a fyke net in 35 feet of water south of Saunders Point, Gladstone, Michigan, mature male, 259 millimeters standard length, 318 millimeters (12.5 inches) total length, sent by Roy Jensen.

The first Lake Huron statistics of so-called mooneyes were published by the United States showing that 2,895 pounds, valued at $290, were taken in 1929, but the State of Michigan listed these fishes as shiners. Michigan also reported shiners from Lake Erie in 1929 that were again named mooneyes by the United States. These fishes totaled 701 pounds, valued at $21. The price per pound of these Lake Erie fishes averaged 3 cents but those from Lake Huron averaged 10 cents. It was determined that the only other species from Lake Huron that brought 10 cents per pound was the chub (cisco) and in Lake Erie only the mooneyes brought 3 cents per pound. These 1929 prices indicate that the above-mentioned Lake Huron specimens were apparently "mooneye" chubs and the Lake Erie fishes were real mooneyes.

The next Lake Huron record of mooneyes published by the United States listed 330 pounds caught in 1934 north of Lexington, Michigan. These fishes, however, were identified as gizzard shad. The State of Michigan did not include these fishes either as mooneyes or gizzard shad in its published statistics. Not until 1949 were mooneyes again reported from Lake Huron when 52 pounds were recorded from the Saginaw Bay area. Perhaps the average prices may again identify these mooneyes as gizzard shad. Mooneyes were sold for 5 cents per pound, shad for 2 or 3 cents. Since the prices of both the mooneyes and gizzard shad of Lake Huron averaged 2 cents per pound, all of these fishes were no doubt real shad. In 1951 mooneyes that weighed only 1 pound were again recorded from Saginaw Bay although not identified by an authority.

The next statistics of Lake Huron mooneyes indicated an increasing yield from 255 pounds (actually 875 pounds) in 1956 to 13,663 pounds in 1958 when it surpassed the maximum reported production of gizzard shad (6,483 pounds). All of these mooneyes were taken from Saginaw Bay by certain fishermen of one of the companies, although the rest of the companies as well as other fishermen listed only gizzard shad. Gizzard shad were caught on the same grounds where the mooneyes were taken. It is of interest to note that the United States research vessel *Cisco* had not taken a single mooneye in 1956 in the experimental nets operated in Saginaw Bay and southern Lake Huron. However, tremendous numbers of alewives were caught. I have now been informed (spring, 1960) that the alewives of Saginaw Bay had actually been called mooneyes since 1956.

The facts that the gizzard shad had been taken from Lake Huron off Sarnia, Ontario, as early as 1877 (Wilmot, 1879) and commercialized every year since 1938 indicate that the reported mooneyes were usually gizzard shad, although recently were alewives. The statistics did not reveal the abundance of these Lake Huron shad and alewives because most of them had not been marketed. Swarms of gizzard shad had already been observed before the years when they had been sold, as for example, in Georgian Bay 1919, in Saginaw Bay 1920, 1932, 1933, and 1937, off Alpena, Michigan, 1932 and 1933, in Lake St. Clair and St. Clair River 1932 and 1933, off Goderich, Ontario, 1933, and off Harbor Beach, Michigan, 1933. When they suddenly increased in numbers, they periodically underwent heavy mortality.

The real mooneyes of the Great Lakes are most abundant in the Ohio waters of Lake Erie. They were listed in published statistics for the first time in 1899 at 43,836 pounds, the maximum record. Thereafter statistics were published for the years 1918–21, 1927 (Michigan), and continuously from 1929. The Lake Erie annual catch averaged 5,441 pounds during 1918–21, 12,753 pounds during 1929–56, and only 500 pounds in each year of 1957 and 1958, the minimum production. Whether the early statistics of the mooneyes had included gizzard shad may be somewhat doubtful because the production of the shad had not been recorded until 1935, although not every year thereafter.

Scientific records indicate that mooneyes are also rather common in Lake Ontario and the St. Lawrence River, but they apparently have not been marketed since they have not

TABLE 1.—*Ports, dates of capture, and number of Lake Erie mooneyes in various age groups, 1927–29*

[Number of specimens in parenthesis may have been taken from more than one location]

Age group	Number of fish	Ports	Periods of capture
I	31	Sandusky, O.	Sept. 15—Nov. 5, 1927 (19)
		Huron, O.	Aug. 10—Nov. 27, 1928 (9)
		Conneaut, O.	May 15, 27, 1929 (3)
II	5	Sandusky, O.	Sept. 15—Oct. 31, 1927
III	9	Sandusky, O.	Aug. 26—Sept. 26, 1927
		Vermilion, O.	
IV	5	Toledo, O.	Sept. 12, 1927 (1)
		Sandusky, O.	Nov. 13, 27, 1928 (4)
		Vermilion, O.	
V	7	Toledo, O.	Aug. 19—Sept. 15, 1927 (4)
		Sandusky, O.	Nov. 13, 27, 1928 (2)
		Vermilion, O.	May 15, 1929 (1)
VII	1	Toledo, O.	Nov. 13, 1928
2.24[1]	58[2]	All ports	1927–1929

[1] The average number of annuli of all age groups.
[2] Two of age-group III, one of IV, and one of V were taken in 1927 in shoal gill nets; one of V caught in 1927 in a bullnet; all other specimens were taken in trap nets.

been listed in the United States statistics unless included in the miscellaneous species that were published in the 18 years during the period from 1879 to 1928.

Very little information has been published about the life history of the Great Lakes mooneye, the only species of its family in these lakes. Boesel (1938) listed the stomach contents of Lake Erie mooneyes. Those smaller than 40 millimeters had contained Entomostraca and the larger individuals (57–133 millimeters) had consumed insects and amphipods. Johnson (1951) reported general information on 650 mooneyes from Lake Erie and Lake St. Clair. His data showed fork length from 7 to 13½ inches, weights from 3 to 18 ounces, ages from 1+ to 8+ years, and eggs from 10,000 to 20,000 per female. Stomachs contained aquatic and terrestrial invertebrates, mostly insects. Spawning occurred in April and May. Trautman (1957) recorded that the young-of-year mooneyes of Ohio ranged from 4.5 to 6.5 inches in October and adults usually varied from 11.0 to 15.0 inches and from 12 ounces to 2 pounds. He did not indicate that all of these measurements applied to the Lake Erie mooneyes. During our Lake Erie investigations mooneyes were recorded in the samples of 1927–31, and some detailed data and scales were collected.

Our records indicate that the mooneyes were not abundant in Lake Erie and virtually all were caught in trap nets, pound nets, and seines in depths less than 35 feet. Only one specimen was taken in a bullnet in 42 feet of water and four in shoal gill nets in depths

TABLE 2.—*Standard and total lengths, weights, and calculated standard lengths based on radius and diameter measurements of the age groups of Lake Erie mooneyes, 1927–29*

[Specimens of different years and ports have been combined; numbers of specimens in parentheses]

Age group	Number of fish[1]	Average standard length (millimeters)	Computed total length (inches)[2]	Average weight (ounces)		Average calculated standard lengths for each year computed from scale dimensions						
						1	2	3	4	5	6	7
I	31	177	8.4	2.91	Radii[3]	91						
					Diameters[3]	106						
II	5	203	9.6	4.25	Radii	97	159					
					Diameters	114	166					
III	9	244	11.6	8.06	Radii	87	173	220				
					Diameters	106	181	222				
IV	5	257	12.2	10.30	Radii	81	156	203	236			
					Diameters	95	168	207	239			
V	7	265	12.6	11.18	Radii	73	151	199	234	254		
					Diameters	90	160	203	236	255		
VII	1	276	13.1	12.75	Radii	77	170	219	237	254	262	268
					Diameters	82	181	215	242	252	262	270
2.24[4]	58[5]	209	9.9	5.63	Radii	87	161	210	235	254	262	268
					Diameters	103	170	212	238	255	262	270
						(58)	(27)	(22)	(13)	(8)	(1)	(1)
Total length (inches)					Radii	4.1	7.6	10.0	11.1	12.0	12.4	12.7
					Diameters	4.9	8.1	10.1	11.3	12.1	12.4	12.8
Increments (inches)					Radii	4.1	3.5	2.3	1.2	0.9	0.4	0.3
					Diameters	4.9	3.2	2.0	1.2	0.8	0.3	0.4
Increments (millimeters)					Radii	87	74	49	25	19	8	6
					Diameters	103	67	42	26	17	7	5

[1] Sexes were combined since only six males and nine females were recorded.
[2] Standard length × 1.206 equals total length.
[3] Radius of anterior section and diameter of lateral areas.
[4] The average number of annuli of all age groups.
[5] See footnote 2, Table 1.

TABLE 3.—*Length–weight relationship of the Lake Erie mooneyes, 1927–31*

Range total length (inches)	Average total length (inches)	Average standard length (millimeters)	Average weight (ounces)	Number of fish
5.5– 5.9	5.6	119	0.75	2
6.0– 6.4	6.2	130	0.94	4
6.5– 6.9	6.8	143	1.67	3
7.0– 7.4	–	–	–	–
7.5– 7.9	7.8	165	2.53	9
8.0– 8.4	8.2	173	2.78	8
8.5– 8.9	8.7	183	3.12	35
9.0– 9.4	9.1	192	3.76	22
9.5– 9.9	9.6	202	4.57	7
10.0–10.4	10.1	213	5.12	10
10.5–10.9	10.8	228	6.67	3
11.0–11.4	11.2	237	7.88	6
11.5–11.9	11.7	246	8.61	7
12.0–12.4	12.1	256	10.25	6
12.5–12.9	12.7	267	10.95	5
13.0–13.4	13.2	278	12.35	5
13.5–13.9	13.6	286	12.38	2
14.0–14.4	–	–	–	–
14.5–14.9	14.5	306	14.75	1
5.5–14.9	9.6	201	5.00	135[1]

[1] 113 taken in trap nets (Sandusky 76, Huron 28, Conneaut 5, Toledo 4), 17 in pound nets, Erie, Pa., 4 in shoal gill nets and 1 in a bullnet in Vermilion, O. 63 were taken in 1927, 22 in 1928, 46 in 1929, and 4 in 1931.

42–56 feet, although we had collected random samples from approximately 5,616 bullnets and 11,520 shoal gill nets. Similarly, only a few units of the other gear fished caught mooneyes. Only 130 of the 1,493 trap nets had taken 634 mooneyes (average 4.9), 16 of 669 pound nets had caught 17 specimens (average 0.9); and the several random samples of the two seines (Sandusky Bay) included 33 mooneyes (average 16.5). Our mooneyes had been distributed along the entire shore from Toledo, Ohio, to Erie, Pennsylvania.

Scales of 58 mooneyes were collected from various ports (Table 1). Age groups ranged from I to VII, and 53 percent of the fish belonged to age-group I. The average total lengths and weights of the different age groups varied from 8.4 to 13.1 inches and 2.91 to 12.75 ounces(Table 2). Comparisons were made of the calculated standard lengths based on the anterior radii and lateral diameters of the scales. Because the annuli were not formed in the posterior area beyond the second or third summer the anterior–posterior diameters were not usable. Figure 1 shows one of the very few scales that revealed posterior circuli throughout the third year although the marginal part is relatively transparent.

The calculated standard and total lengths were greater when computed from diameters than from radii, although the differences were not significant after the second year. The

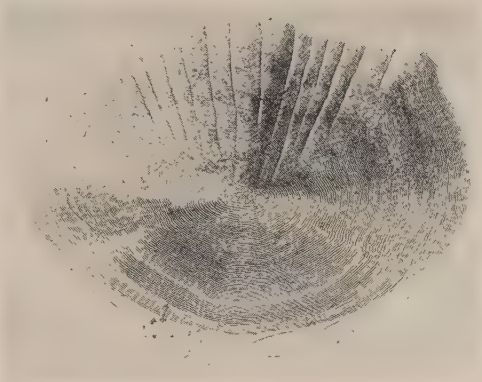

FIGURE 1.—Scale of Lake Erie mooneye, female, age-group II, two annuli, total length 8.8 inches, 2.75 ounces. September 15, 1927, Sandusky, Ohio. (Photographed by Clifford Tetzloff.)

results were due almost entirely to the increments of the first year when the two general averages differed 16 millimeters (0.8 inch). Throughout nearly all of the later years the increments computed from radii were greater but not enough to counteract the results of the first year. The grand average calculated lengths, especially those based on diameters, were decreased no more than 0.3 inch from the virtually completed actual lengths of the same age groups.

The length–weight relationship of 135 mooneyes collected in 1927–31 is shown in Table 3. They ranged from 5.6 to 14.5 inches total length and from 0.75 to 14.75 ounces. Twenty-six percent of these specimens ranged from 8.5 to 8.9 inches and averaged 8.7 inches in total length and 3.12 ounces in weight. Those that ranged from 8.5 to 9.4 inches constituted 42 percent and averaged 8.8 inches total length and 3.37 ounces in weight. The entire group averaged 9.6 inches and 5.0 ounces.

The sexual maturity of only 19 mooneyes was reported. Seven were males, nine females, and three immature unknown sexes. All nine of age-group I and the two of age-group II were immature. The remaining eight mooneyes were mature, five of them 3 years, and two, 5 years old. It appears that none of the immature specimens exceeded 8.8 inches and 3.25 ounces.

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Natural Mortality of American Shad

CHARLES H. WALBURG

Natural Mortality of American Shad[1]

Since 1950 the Bureau of Commercial Fisheries has studied the American shad (*Alosa sapidissima*) of the Connecticut River to obtain information whereby the population may be managed to obtain optimum sustained yields. A necessary part of these investigations is the determination of the natural mortality of adult fish.

Few studies have been conducted to determine natural mortality of shad. Fredin (1954) compared the estimated abundance of 6- to 7-year-old fish collected in the Connecticut River in 1946 and 1947, and estimated that the extraneous mortality rate (deaths occurring between fishing seasons) was 36 percent. Talbot and Sykes (1958) reported that adult shad native to streams south of Cape Hatteras, North Carolina, die after spawning. The natural mortality of these fish after initial spawning is presumed to be 100 percent.

In the Connecticut River over 80 percent of the fluctuations in size of runs can be attributed to changes in the size of the escapement from the fishery (Fredin, 1954). Therefore, the number of progeny is dependent on the size of the spawning stock. Using catch and effort statistics supplied by the Connecticut State Board of Fisheries and Game, Fredin presented a method whereby total effort in standard fishing units, fishing mortality rate, and population size could be determined annually. These data are available for each year 1935 to 1959.[2]

In addition to the Connecticut River fishery, shad native to this stream are captured along their ocean migration routes from North Carolina to Maine (Talbot and Sykes, 1958). It was estimated by Nichols (1958) that approximately 13 percent of the 1956 shad catch taken by the New York–New Jersey ocean pound-net fishery (16,000 fish) was native to the Connecticut River. It was further pointed out by Nichols that each year during the summer and fall, large numbers of ocean-migrant shad are taken incidentally in the Gulf of Maine by purse seiners.

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[1] Part of the shad investigation being conducted by the Bureau of Commercial Fisheries to furnish information to the Atlantic States Marine Fisheries Commission.

[2] 1935–51, Fredin (1954); 1952–59, unpublished data, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina.

TABLE 1.—*Number of shad in each age group caught per 100 standard units of fishing effort, Connecticut River*

Year	Age group III	IV	V	VI	VII	VIII	IX
1956	25	2,202	1,698	1,913	283	25	0
1957	114	975	5,448	1,485	545	193	18
1958	19	1,714	2,775	3,983	720	419	78
1959	18	1,039	4,417	2,728	816	223	46
Average number	44	1,482	3,584	2,527	591	215	36
Natural log of average number	3.784	7.301	8.184	7.835	6.382	5.371	3.584

TABLE 2.—*Number of shad in each spawning group*[1] *caught per 100 standard units of fishing effort, Connecticut River*

Year	Spawning marks 0	1	2	3	4	5
1956	3,610	1,849	639	146	34	0
1957	5,413	2,221	891	217	111	0
1958	4,200	3,250	1,671	610	153	42
1959	4,337	3,271	1,297	338	100	39
Average number	4,390	2,648	1,124	328	100	20
Natural log of average number	8.387	7.909	7.025	5.793	4.605	2.996

[1] Spawning group denotes number of spawning marks.

Causes of mortality of adult shad native to the Connecticut River, exclusive of that from fishing within the river, are: (1) natural causes during or following spawning within the river; (2) natural causes at sea; and (3) fishing outside of the river. These mortalities were grouped and termed natural mortality. The natural mortality rate plus the river fishing mortality rate is equivalent to the total mortality rate (Ricker, 1958). Since annual estimates of the fishing mortality rate are available, the natural mortality rate can be determined if the total mortality rate is known.

MATERIALS

Shad scales were collected in the Connecticut River throughout the 1956–59 fishing seasons (April 1 to June 15 of each year) to obtain samples which were representative of the catch. From 1956 through 1959, 720, 531, 582, and 616 shad were sampled in the respective years. Length, weight, and sex were determined, and plastic impressions of two scales from each fish were read by two biologists using an Eberbach projector. Less than 1 percent of the scales were discarded as unreadable. Total age and number of times spawned were determined for all fish. Annuli and spawning marks as age indicators of shad have been validated.[3]

MORTALITY DETERMINATIONS

Total mortality estimates were obtained from both age- and spawning-group frequencies during the period 1956–59. A number of assumptions underlie this method of mortality estimation. According to Rounsefell and Everhart (1953) they are: (1) annual recruitment to the population was constant at the time each age group entered the fishery; (2) ages can be deciphered with a high degree of accuracy; (3) natural mortality has been constant over the period involved; (4) fishing mortality has been uniform over the period involved; (5) mortality rate of fully vulnerable age groups is equal between age groups; and (6) age samples are representative of the vulnerable age groups. These assumptions appear reasonably satisfied in this study, but as pointed out by Ricker (1958) rarely are all the theoretical requirements fulfilled.

The catch by age and spawning group for each year adjusted to 100 standard fishing units of effort was determined (Tables 1 and 2). Because there were fluctuations in year-class strength, the age- and spawning-group distributions for the 4 years were combined to obtain an estimate of average abundance. Beverton and Holt (1956) state that average abundance can be used to obtain an approximation of total mortality if the assumption is made that natural mortality is fairly constant over the period under consideration.

Shad native to the Connecticut River spawn for the first time at 3, 4, or 5 years of age. Since age-group VI is the first age group in which practically no maiden fish occur and in which all fish are fully vulnerable to capture, only frequencies of age-groups VI through IX were used to determine total mortality rate (Table 1). Some shad spawning for the first or second time (0 or 1 spawning mark on scales) are not large enough to be fully vulnerable to capture by the commercial fishery. Only fish with two or more spawning marks, therefore, were used to determine total mortality from spawning-group frequencies (Table 2).

Total mortality rates were calculated from the average age- and spawning-group distributions by a method of Rounsefell and

[3] Judy, Mayo H. (Manuscript) Validity of age determination from scales of marked American shad. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina.

Everhart (1953). The estimated total instantaneous mortality rate was 1.35 using age-group frequencies and 1.27 using spawning-group frequencies, or an average of 1.31. The instantaneous rate was converted to an annual rate of 73 percent (Ricker, 1958). If the average annual fishing mortality rate is known for the period under consideration, then the average annual natural mortality rate can be determined from Ricker's (1958) formula:

$$a = m + n - mn$$

where a is the annual total mortality rate, m is the annual fishing mortality rate, and n is the annual natural mortality rate. From unpublished data[4] it was calculated that the average annual fishing mortality rate on shad fully vulnerable to capture (fish larger than 16.7 inches fork length) over the period 1956–59 was 36 percent (range 30–40 percent).[5] The estimated average annual natural mortality rate during the period 1956–59 was therefore 58 percent.

The high natural mortality rate of adult shad is verified by the scarcity of older age groups in the catch and the preponderance of newly matured fish. This phenomenon has been found not only for the Connecticut River population but also for all Atlantic coast populations south to Chesapeake Bay.

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Bureau of Commercial Fisheries
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[4] Bureau of Commercial Fisheries Biological Laboratory, Beaufort, North Carolina.

[5] Includes both sport and commercially caught fish.

SYMPOSIUM ON FISHERY PROTECTION
IN RELATION TO DAMS AND
WATER DEVELOPMENT PROJECTS

The Status of Fish Passage in the Pacific Northwest

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In the Pacific Northwest, population increase and industrial growth have required extensive development of water resources during the past two decades. The expanding economic base of the region demands development of hydroelectric power, flood control, inland waterway transportation, and irrigation. One of the prime natural resources has always been the abundant runs of salmon and steelhead trout which spawn in the gravel bars and riffles of the cool, snow-fed streams.

The Columbia River Basin, which drains more than one quarter million square miles of the United States and Canada and extends 1200 miles from headwaters to the Pacific Ocean, has long been the focus of this water resource development. Normally over one hundred million acre feet of water flow annually into the ocean. Many dams have been built to control and utilize this water resource. Some have elaborate fishways and some have none at all.

To keep pace with rapid economic growth in the Columbia River Basin, the U. S. Army Corps of Engineers, working closely with Federal and state agencies, prepared and submitted in 1948 a comprehensive water resource development plan. Subsequently, four multipurpose dams have been constructed and two are under construction on the main-stem Columbia River. Two are under construction and one has been completed on the Snake River. All of these recent projects except the uppermost Snake River dam are river-run projects, *i.e.*, water is not stored for long periods of time in their reservoirs which are primarily to create operating heads for hydroelectric plants. Even so, they create a series of semi-slack-water pools where formerly a stream environment existed. The modified physical features of the river alter the ecological habitat of all aquatic life and create fish passage problems. Salmon and steelhead comprise many races, each adapted over many years to specific environmental conditions. Successful spawning depends upon rather precisely timed migrations and arrival at suitable spawning grounds. Until recently, facilities for fish passage have been provided only at relatively low-head dams. Impassable dams and flooded spawning grounds have reduced available Columbia Basin spawning grounds by about 70 per cent.

Fish passage research and fishery science have not kept pace with water resource development in general. Evidence of this lag is becoming more and more obvious as research discloses new fishway design criteria. Recent studies have explored fishway capacity, slope, length, and hydraulics. Swimming ability, endurance and some preferences of fish have been tested.

Search for knowledge to provide safe passage for downstream migrants has included behavioral studies, explorations to determine cross sectional distribution of fingerlings in reservoirs, determination of the effects of passage through turbines and spillways, development and testing of guiding and collecting systems, and tests of transportation methods.

Recent construction of several high-head dams and plans for additional ones on the migration routes of valuable salmonoids emphasize urgency for knowledge regarding fish passage. Vast and deep slack-water pools behind these dams present grave, new problems to the fishery scientists. Supplemental funds have been assured and research is gaining much needed momentum in the Pacific Northwest.

IN: Abstracts of symposium papers Tenth Pacific Science Congress, Honolulu, Hawaii, 1961, p. 151-152.

FLATWORM DISTRIBUTION AND ASSOCIATED OYSTER MORTALITY IN CHESAPEAKE BAY

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Annapolis, Maryland

ABSTRACT

The marine flatworm Stylochus ellipticus (Girard) is reported from 73 widely scattered localities in Maryland Chesapeake Bay and its tributaries. It is the only polyclad turbellarian so far identified in dredgings from oyster beds within that area. Occasionally found in fresh spat boxes, the worm is considered to be a predator of oyster spat in the Bay. Evidence for worm predation on small oyster spat is presented. Of the 567 worms found in 90 seed-oyster samples, about 95 per cent were recovered from fresh spat boxes. Statistical treatment of the data concerning worm incidence and recent spat mortality indicated the probability that such mortality resulted from predation by S. ellipticus.

INTRODUCTION

Although the marine flatworm, Stylochus ellipticus (Girard), has been known to occur in Chesapeake Bay for some time, little attention has been given to its potential as a predator of oyster spat. In view of this, a systematic collection of this species was started in 1958 to determine its distribution and possible association with oyster spat mortalities.

DESCRIPTION OF THE WORM

The largest specimens of S. ellipticus collected in Maryland Chesapeake Bay measure about 25 mm. The worm is oval, leaf-like, flat and thin with undulating margins. The most common color is brown, but dark pink, orange and olive drab worms have also been observed. The ventral surface is usually lighter than the dorsal. There is commonly a median dorsal stripe of lighter color athwart which are paired tentacles near the anterior end. There are numerous ocelli (eye spots) around the anterior margin and on the tentacles. The mouth, with its short pharynx, is situated about 1/3 back from the anterior end of the body on the ventral side. The pharynx may be everted to a considerable distance. The intestine has many branches and terminates in a fine network along the edges of the worm. Male and female genital pores, situated close together near the ventral posterior margin, pro-

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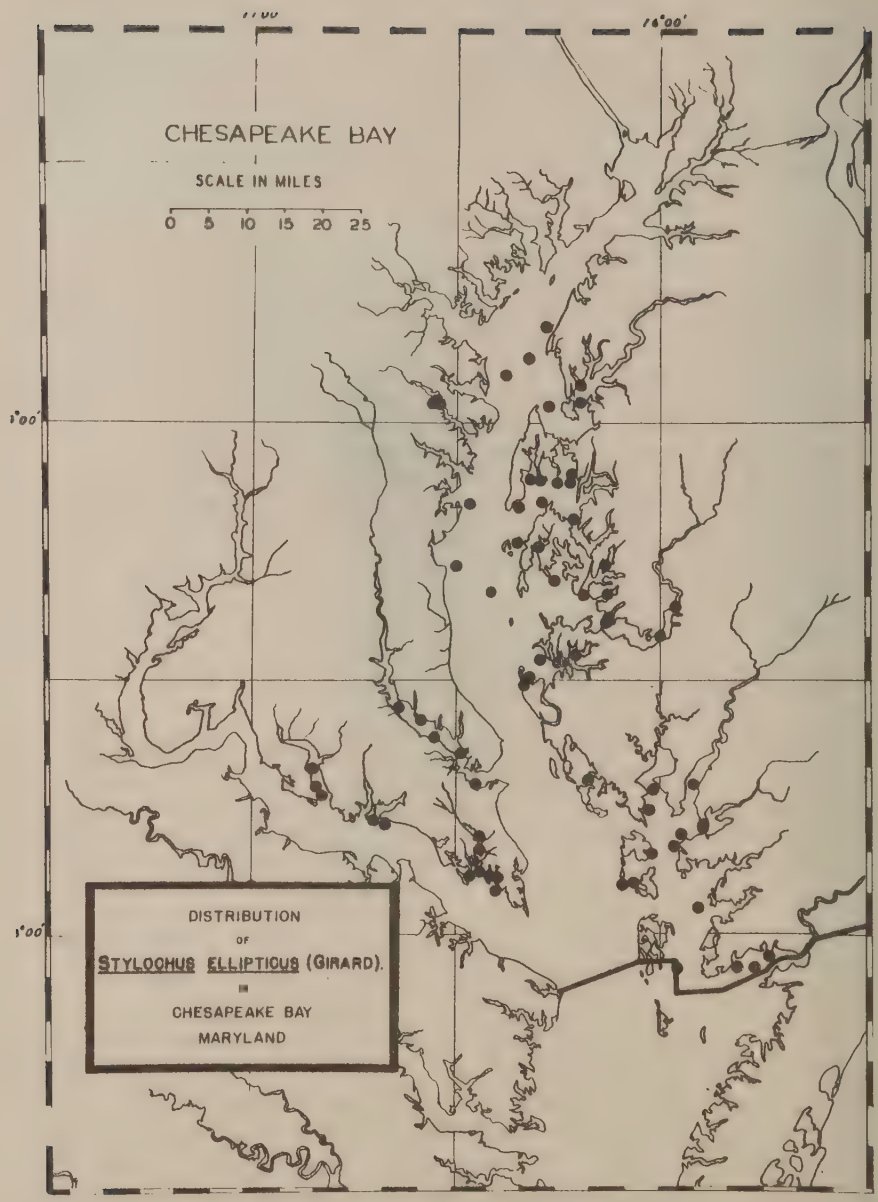
CHESAPEAKE BAY
SCALE IN MILES
0 5 10 15 20 25
DISTRIBUTION
OF
STYLOCHUS ELLIPTICUS (GIRARD).
IN
CHESAPEAKE BAY
MARYLAND

Fig. 1.

vide for sexual reproduction. Hyman (1940) gives a detailed taxonomic description of this species.

DISTRIBUTION OF STYLOCHUS ELLIPTICUS IN MARYLAND CHESAPEAKE BAY

The geographical range of this species, as listed by Hyman (1940), is from Prince Edward Island to Texas. Pearse (1938) records the presence of S. ellipticus from a number of localities in Chesapeake Bay and Engle (unpublished field data) reported this species fairly abundant on oyster beds in the Bay as early as 1944.

Our present collection was started in 1958. Most specimens were found in samples of bottom material dredged during spring oyster-population surveys. These surveys included dredgings on some of the public oyster beds in Maryland Chesapeake Bay and most of its tributaries. The actual finding of worms in these dredgings was incidental to counts bearing upon the age composition of oyster populations. Thus, while the collection data are not quantitative, the survey records show that flatworms were present at 73 widely scattered localities in the Maryland Chesapeake Bay (Figure 1).

The total number of worms collected on the baywide surveys since 1958, about 150, is small in comparison with their broad distribution. Within limits of our collection methods, however, Stylochus has been found in greatest numbers on oyster beds in the lower Potomac River and its immediate tributaries. Hyman (1940) reports that the habitat of this species is littoral and that it is generally found among oysters and old shells, barnacles, and under rocks. The data presented in this paper relate only to flatworm distribution on oyster beds in the Bay.

EVIDENCE OF PREDATION

Sometimes during oyster-bed surveys flatworms were found in fresh oyster spat boxes (hinged valves with clean inner faces but no meat). Pearse and Littler (1938) and Hyman (1940) consider S. ellipticus to be an oyster predator. Pearse and Wharton (1938) demonstrated that a related species, Stylochus frontalis (=inimicus), is an active oyster enemy in Florida. Loosanoff (1956) has shown in laboratory experiments that S. ellipticus feeds on oyster spat. In one experiment, 10 worms consumed 21 spat in less than one month. Although other members of the genus Stylochus may be present in Chesapeake Bay, S. ellipticus appears to be the dominant species of polyclad turbellarian common to oyster beds in the Maryland part of the Bay. It was the only species present in our collections as identified by Dr. Libbie H. Hyman of the American Museum of Natural History. Thus, while attacks by flatworms against healthy oysters were not specifically observed, our finding of worms in fresh spat boxes certainly suggests that predation of

oyster spat by S. ellipticus does occur in Chesapeake Bay.

The contention that predation of oyster spat by flatworms may be common in the field is supported by the relationship of worm distribution and spat mortality. The data were obtained in conjunction with an oyster-seed production experiment conducted in 1958 at Smith Creek, a tidal estuary of the Potomac River.

Wire bags, each containing one-quarter bushel of oyster shells, were suspended in vertical strings at 10-foot intervals along a 240-foot transect running outward from the shore across grounds planted with shell. Depths ranged from 3 feet at the inshore end to about 8 1/2 feet at the offshore end of the transect. Most strings accommodated 4 bags arranged at various depths between surface and bottom. The entire transect was represented by 90 bags.

After removal of bags in the fall, they were examined and counts were made of living spat (a measure of survival after setting) and spat boxes (an approximate measure of recent spat mortality). A search was made for flatworms on shells, in spat and in all spat boxes. Some bags were free of worms; in others the count ranged as high as 19. In all, 567 worms were found for an average of about 6 per bag. Nearly 95 per cent of the worms were found in fresh spat boxes, the remainder occurring elsewhere on culch shells or in the debris on the examining table. In most cases, worms were not present in spat boxes whose inner faces were covered with fouling growth or silt.

RELATIONSHIP BETWEEN SPAT MORTALITY AND WORM INCIDENCE

Spat-box counts were limited to material from 26 bags distributed throughout the transect. These counts showed a positive correlation between the percentage of boxes in the total of spat and boxes together and the numbers of worms per bag. The coefficient of this correlation was + 0.58. Linear regression variance was summarized as follows:

	DF	SS	MS	F	1% Point
Explained by regression	1	1544	1544	12.1	7.82
Unexplained deviations	24	3056	127		
Total	25	4600			

Apparently the relationship between spat mortality and worm incidence was not a consequence of chance alone. A scatter diagram of the correlation points, with the line of regression determined by the method of least squares, is shown in Figure 2.

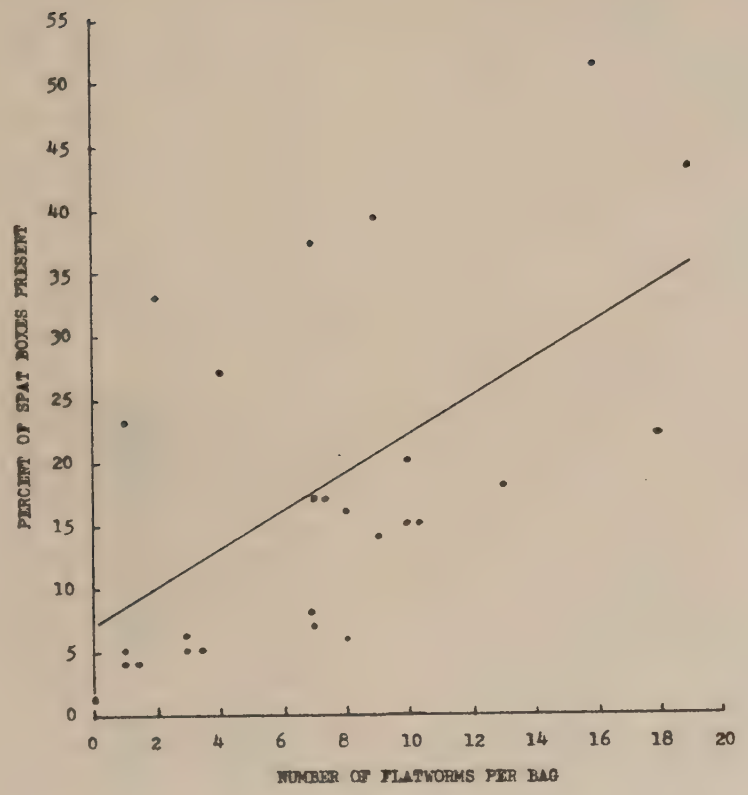

Fig. 2. Correlation of Flatworm Incidence and Recent Spat Mortality.

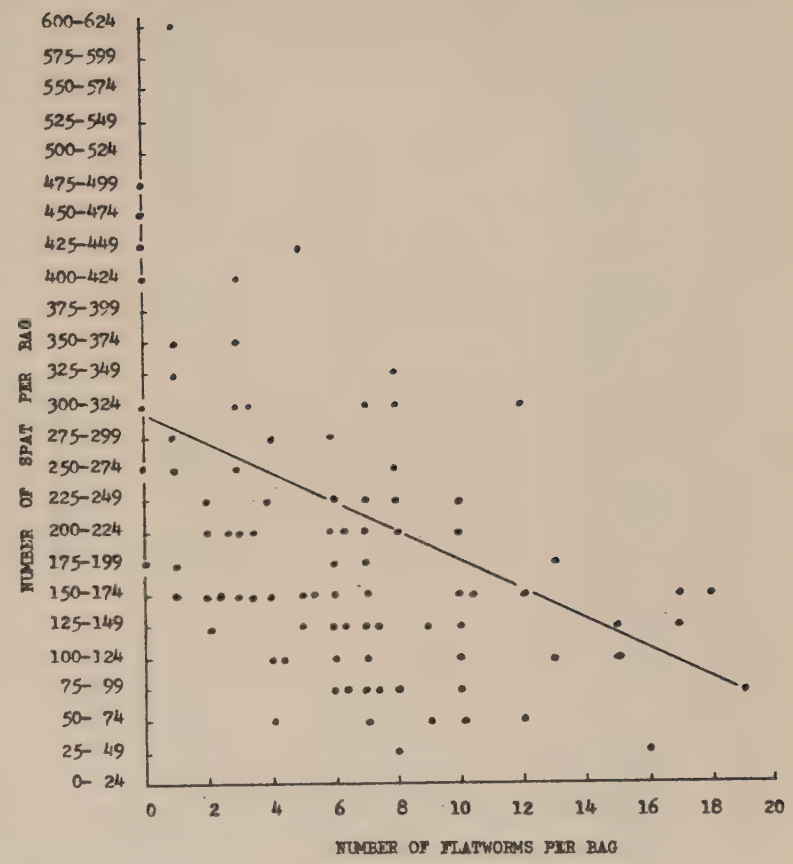

Fig. 3. Correlation of Flatworm Incidence and Spat Survival.

RELATIONSHIP BETWEEN SPAT SURVIVAL AND WORM INCIDENCE

Counts representing spat survival and worm incidence for all 90 bags were treated without regard to bag position in the transect. Here, a coefficient of correlation of approximately - 0.49 was calculated. Despite this low coefficient, a simple analysis of variance showed high probability that the relationship was not a consequence of chance. In this instance:

	DF	SS	MS	F	1% Point
Explained by regression	1	264256	264256	28.2	6.96
Unexplained deviations	88	824883	9374		
Total	89	1089139			

A scatter diagram of the ralationship between spat survival and worm incidence, with the line of regression calculated by the method of least squares, is shown in Figure 3.

CONCLUSIONS

Our field collections prove that the turbellarian flatworm, Stylochus ellipticus, occurs widely in the Maryland Chesapeake Bay and its tributaries. Recovery of worms from fresh oyster boxes, mostly spat, suggests a predatory relationship in explanation of many oyster mortalities. The evidence is circumstantial but corroborates reports of predation by investigators elsewhere. Returns from a seed-oyster production experiment in southern Maryland show that the vulnerability of oyster spat to flatworm predation could be real and markedly detrimental to seed production. The possibility is substantiated by the statistical association between three sets of numbers, one representing flatworm incidence, another representing spat mortality and the third representing the rate of spat survival during the summer.

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A NEW ISOPOD, *CHIRIDOTEA NIGRESCENS*, FROM CAPE COD, MASSACHUSETTS

BY

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Bureau of Commercial Fisheries, Biological Laboratory, Woods Hole, Massachusetts

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A NEW ISOPOD, *CHIRIDOTEA NIGRESCENS,* FROM CAPE COD, MASSACHUSETTS

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The genus *Chiridotea,* family Idoteidae, is composed of a small number o species which occur along the eastern coast of North America from Florida t Nova Scotia. The new species introduced here constitutes the fifth known membe of this genus. Previously described species are *C. coeca* (Say, 1818), *C. tufts* (Stimpson, 1853), *C. almyra* Bowman (1955), and *C. arenicola* Wigley (1960) This group of isopods are bottom-dwelling forms that usually inhabit sandy sedi ments. They have the curious habit of burrowing horizontally just below th sediment surface. Three of the species mentioned have been reported only fron strictly marine environments; the other, *C. almyra.* is a brackish water form. Th new species described here is also a brackish water inhabitant.

Chiridotea nigrescens[1]) new species (figs. 1, 2, 3)

Material examined:

Old Silver Beach, town of Falmouth, Massachusetts; January 31, 1960; 1 male, body lengt 8.0 mm; 5 females, body lengths 7.0 to 8.0 mm (holo- and paratypes).

Old Silver Beach, town of Falmouth, Massachusetts; February 13, 1960; 4 males, body length 7.5 to 10.5 mm; 7 females, body lengths 4.0 to 8.5 mm (paratypes).

Sippewissett, town of Falmouth, Massachusetts; February 13, 1960; 8 males, body lengths 7.5 t 10.0 mm; 2 females, body lengths 6.5 and 7.0 mm.

Sippewissett, town of Falmouth, Massachusetts; February 20, 1960; 3 females, body length 6.0 to 8.0 mm.

Sippewissett, town of Falmouth, Massachusetts; May 25, 1960; 11 females, oostegites developec body lengths 7.0 to 10.0 mm; 3 males, body lengths 7.0 to 9.0 mm.

Davisville, town of Falmouth, Massachusetts; May 29, 1960; 3 females, oostegites developec body lengths 7.5 to 8.0 mm.

Chatham, town of Chatham, Massachusetts; February 22, 1960; 6 females, oostegites beginnin to develop, body lengths 6.0 to 6.5 mm; 17 males, body lengths 6.5 to 8.5 mm.

TYPES. The holotype is an adult female 8.0 mm in length that was collecte at Old Silver Beach, Massachusetts, January 31, 1960. It has been deposited i the U. S. National Museum (Catalogue No. 106382). Five paratypes, which wer taken in the same collection with the holotype, have also been deposited in th U. S. National Museum (Catalogue No. 106383). Paratypes in this collectio

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[1]) Meaning blackish; from the Latin nigrescere.

consist of 1 male and 4 females, 7.0 to 8.0 mm in length. A second sample of paratypes collected at Old Silver Beach, Massachusetts, February 13, 1960, are in possession of the Biological Laboratory, U. S. Fish and Wildlife Service, Woods Hole, Massachusetts. This lot contains 4 males 7.5 to 10.5 mm in length, and 7 females 4.0 to 8.5 mm in length.

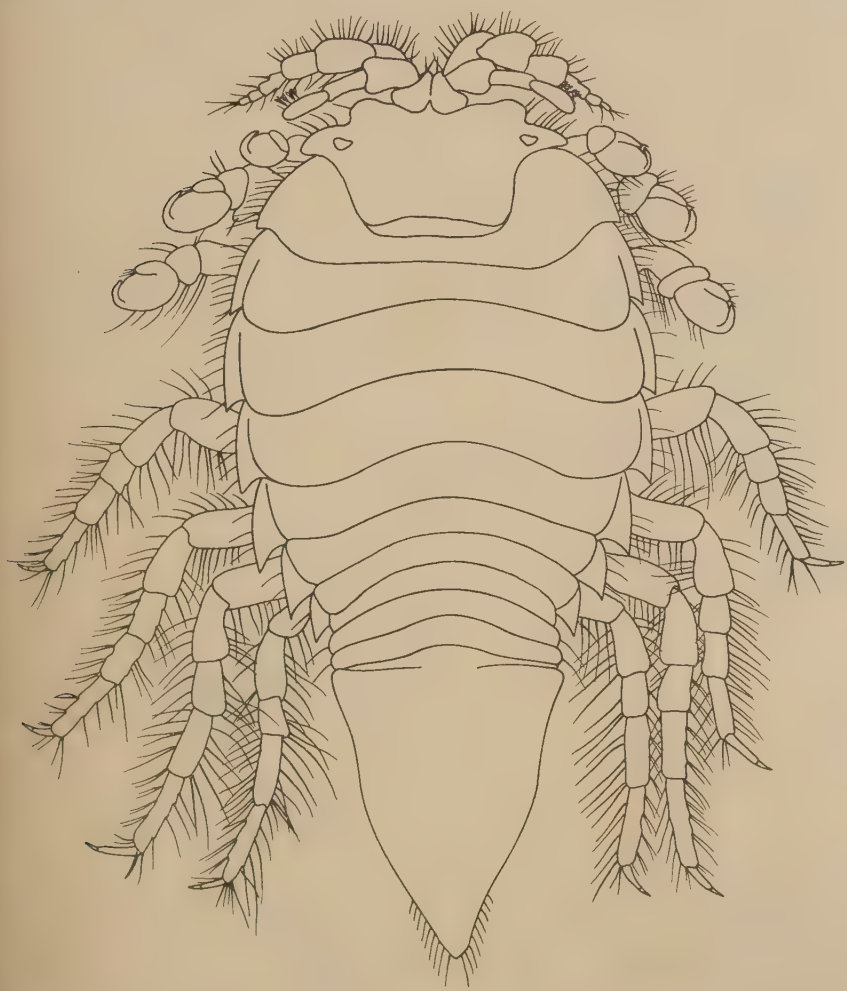

Fig. 1. *Chiridotea nigrescens* new species. Dorsal view of female holotype, body length 8.0 mm.

DIAGNOSIS. Blackish colored, medium-sized species with a broad body and both pairs of antenna short; flagellum of antenna 2 much shorter than the peduncle; antenna 1 slightly shorter than antenna 2; greatest body width one half the body length. This species most closely resembles *C. coeca* (Say), but it is clearly distin-

guishable by its blackish pigmentation, smaller size, shallow clefts in the anterolateral margin of the head, very sparse setation on the outer margin of the anterior lateral lobes of the head, and other characteristics described in a later section of this paper.

DESCRIPTION. Body ovate, twice as long as broad, and tapering to a pointed posterior. Body broadest at thoracic segment 3. Anterior margin of head with a broad, shallow excavation each side of the rostrum. Rostrum tip extends as far

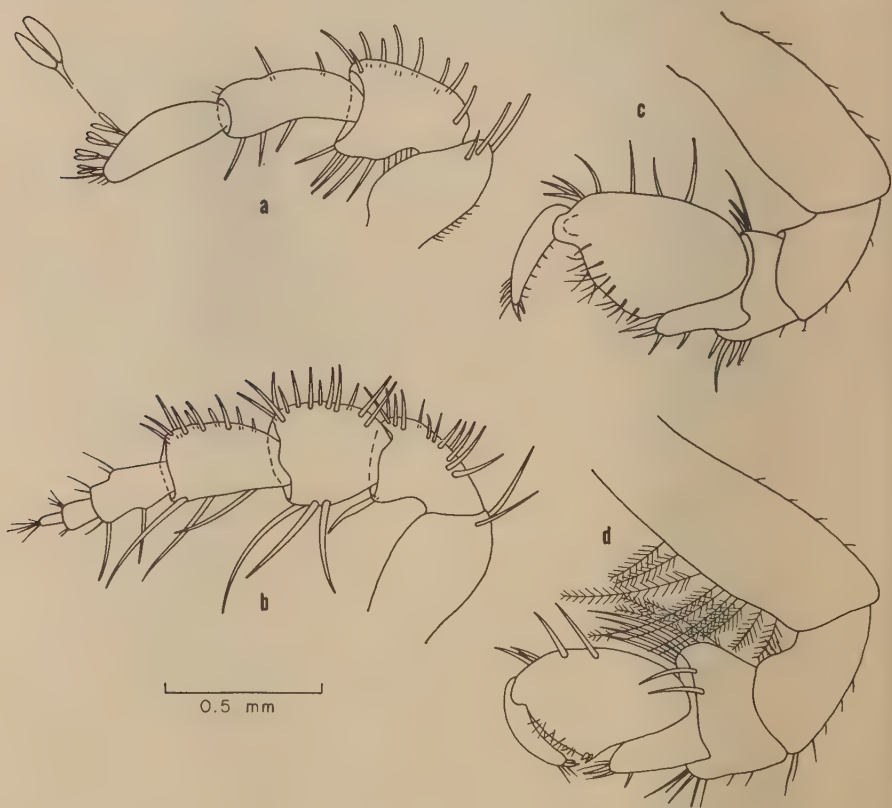

Fig. 2. *Chiridotea nigrescens* new species. a, antenna 1; b, antenna 2; c, pereiopod 1; d, pereiopod 2.

forward as the anterolateral projections on the head. Lateral forward projections on the head are very broad and rounded. Anterolateral margins of the head are divided into two lobes by a very shallow, U- or V-shaped notch. Margin of each anterior lobe usually bears one or two setae; posterior lobes have five to eight setae. Anterior lobes are narrower and shorter than the posterior lobes. Posterior portion of head deeply recessed in the first thoracic segment. Eyes small, irregularly oblong, located dorsally on the head at the base of the posterolateral lobes.

Eyes are not evident in preserved specimens (see section describing color). Epimeral plates distinct on pereion somites 2-7. Lateral margins of pereion somite 1 and epimeral plates 2-7 are slightly convex, fringed with stout setae and, except for somite 1, are acutely produced posteriorly. Pleotelson broad, composed of four

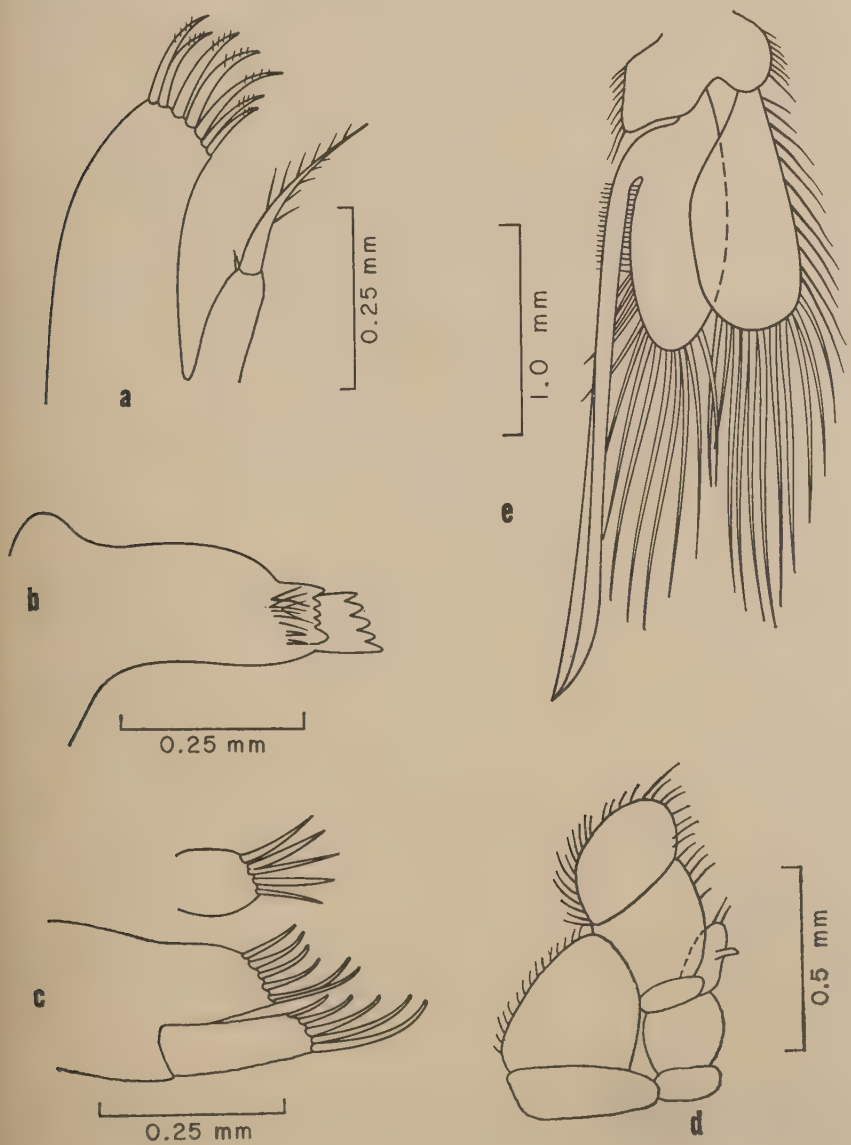

Fig. 3. *Chiridotea nigrescens* new species. a, maxilla 1; b, left mandible; c, maxilla 2; d, maxilliped; e, pleopod 2 from male paratype.

distinct segments with partial separation of another between the third and fourth segments. Lateral margins of the terminal segment taper irregularly to a pointed apex. Lateral margins near the apex are finely denticulate and the posterior 6 to 16 denticles are each furnished with a seta; distal setae are 3 to 5 times as long as the proximal setae.

Body proportions of a few significant dimensions are: body width .49 times body length; pleotelson length .46 body length; head length .16 body length; width at base of terminal segment of pleotelson .27 body length.

Both pairs of antennae short. Antenna 1 extends slightly beyond the terminal end of the peduncle of antenna 2; flagellum a single segment which has two to six pairs of inflated setae on the lower anterior face. Antenna 2 approximately 1.2 times the length of antenna 1, the flagellum is made up of three to six segments, and its length is approximately 1/3 the total antenna length. Maxilliped has a three-segmented palp. Inner lobe of maxilla 1 has two setae; one large and plumose, the other very small and uniramose. Pereiopod 1 has a propodus 1.5 times as long as broad; the occluded margin of the dactyl has about six fine setae; the oblique fringe near the inner distal end of the dactyl is composed of six to eight setae. Pereiopods 1-3 are similar in shape and structure; pereiopods 4-7 are non-chelate and are also similar to one another. The cuticle over almost the entire body and parts of exposed appendages is embellished with sculpturing. This sculpturing, made up largely of irregularly rounded discs of various sizes, is most clearly evident on the head and pleotelson.

Color. The body is distinctly blackish in color due to densely packed, dark chromatophores covering most body surfaces. This pigmentation is also present on many of the larger exposed appendages. Usually the chromatophores are moderately dense at the base of the appendages and diminish toward the extremity. Areas where chromatophores are lacking are cream color or whitish, depending upon tissue thickness. The pigmentation pattern from one specimen to another is quite consistent. The most darkly pigmented areas are the uropods and the mid-dorsal section of the thorax and pleotelson. Dorsal areas that are non-pigmented are: anterolateral lobes of the head, epimeral plates, and the terminal one-fourth of the pleotelson. Eyes of living specimens are silvery-white; however, when placed in preservative they soon fade. After a day or two in formalin the eyes are usually indistinguishable.

Range. Known only from the southern and western shores of Cape Cod, Massachusetts, U.S.A. It has been taken as far north as Old Silver Beach and as far east as Chatham. The presently known range in water temperature is 35° to 74° F.; range in water depth is ½ to 4 feet.

Habitat. *C. nigrescens* inhabits brackish waters of tidal marshes and shallow bays, usually in the channels in clean sand sediments. Occasionally it is found in nearly fully saline water (during an incoming tide), but only near outflows of brackish water and where fresh water seepage is prevalent.

Discussion. Morphologically, *C. nigrescens* is quite similar to *C. coeca*. Some of

the more important species-variable features common to both forms are: short antenna 2, broad pleotelson with sides of the terminal section unevenly tapered, pereiopod 1 with a broad propodus and stout dactyl bearing a few small setae on the occluded margin. Nevertheless, these two species are clearly separable. *C. nigrescens* has the following characteristics which distinguish it from *C. coeca*: (1) It is smaller in size, ranging up to 10.5 mm in body length, whereas *C. coeca* attains lengths up to 13 mm. (2) It is dark in color, nearly black, whereas *C. coeca* is sparsely pigmented. (3) The lobes on the anterolateral margin of the head are separated by a shallow, non-setose notch, whereas *C. coeca* has a deep, setose cleft. (4) The anterior margin of the foremost lateral lobe on the head usually bears 1 or 2 setae (each side), whereas *C. coeca* frequently has between 6 to 10 setae. In addition to these differences, several other morphological factors such as the epimeral setation, globose setae on antenna 1, and the cuticular sculpturing, may also be used for separating these two species.

C. arenicola is the only other species morphologically similar to *C. nigrescens*. Some of the differentiating characteristics which are useful in separating these two species are listed here. As compared with *C. arenicola, C. nigrescens* has the following features: (1) a broader thorax and abdomen; (2) thoracic segment 1 is narrower anteriorly and has more rounded lateral margins; (3) contours of the thoracic margins are more convex, which is enhanced by the shape of thoracic segment 1; (4) pleotelson is much broader, lateral margins of the terminal segment are less evenly tapered, and the apex is more obtusely pointed; (5) pereiopods are shorter and stouter; (6) flagellum and terminal segment of the peduncle of antenna 1 are more elongate; (7) antenna 1 usually extends beyond the distal end of the peduncle of antenna 2; (8) each anterolateral lobe of the head bears 1 or 2 setae; (9) color is much darker; and (10) appendages and epimeral plates are more setose.

Ecologically, *C. nigrescens* is more closely allied to *C. almyra* than to other members of this genus. Both of these species inhabit shallow brackish waters, as opposed to the others which live in strictly marine habitats. Also, it is interesting to note that in regard to body pigmentation, these two species are densely covered with black chromatophores, in contrast to the colorless or sparse pigmentation found in the other species.

Two burrowing invertebrate animals which are frequently found in the same localities with *C. nigrescens* are the amphipod *Haustorius arenarius* (Slabber) and the polychaete *Ophelia bicornis* Savigny. I wish to thank Dr. Marian H. Pettibone, University of New Hampshire, for identifying the polychaete.

RÉSUMÉ

Description d'une nouvelle espèce d'isopode d'eau saumâtre, *Chiridotea nigrescens*. Cette espèce habite les fonds de sable pur dans les marais et les baies peu profondes le long des côtes du sud et de l'ouest du Cape Cod, Massachusetts, États-Unis. *C. nigrescens*, qui ressemble à *C. coeca* (Say), se distingue d'elle par: (1) sa couleur noirâtre, (2) sa petite taille, (3) une entaille non sétifère et peu profonde située de chaque côté de la tête, et (4) une ou deux soies au bord du lobe antéro-latéral de la tête.

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BOTTOM SEDIMENTS OF GEORGES BANK

BY

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FIGS. 1–12, JUNE, 1961

BOTTOM SEDIMENTS OF GEORGES BANK[1]

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ABSTRACT

A survey of Georges Bank bottom sediments was undertaken to provide basic data for use in studying the relationships between substrate composition and the occurrence of benthic animals, especially those which are common foods of fishes.

Particle size composition is the principal sediment character that was studied. Six statistical measures of particle size composition are given in order to designate the main features of the size-frequency distribution of each sample. These measures are: median diameter, mean diameter, coefficient of sorting, kurtosis, and two measures of skewness. In addition to these parameters, organic content, shell content, color, and textural classifications are included. In the presentation and discussion of the data, special emphasis is given to the geographic distribution of the various sediment constituents and particle size composition.

INTRODUCTION

Georges Bank is a relatively shallow portion of the New England continental shelf east of Cape Cod, Massachusetts. It has an area of approximately 12,000 square miles within the 100-fathom isobath. This is a large area, roughly equivalent to 1½ times the area of the Commonwealth of Massachusetts. Water depths between 20 and 100 fathoms occur over most of the bank, and depths over the shoals are 2 to 3 fathoms. Figure 1 is a bathymetric chart of the bank.

This bank is a submerged coastal plain cuesta (Johnson, 1925) with a steep face along the northern perimeter and a gently sloping face to the southward. The original physiography of this cuesta has been revamped by glacial action and more recently by erosion and deposition resulting from water currents.

Objectives of This Survey

Georges Bank is one of the most productive fishing grounds in the world. Hundreds of millions of pounds of fish are harvested from this bank annually and have been for decades. The kinds of fish caught are predominantly bottom-dwelling species such as cod and haddock. Commercial fishermen and biologists familiar with this area are well aware that certain species of fish inhabit only selected areas of the bank. Furthermore, it is known that many benthic invertebrate animals, which are the primary foods for many groundfish, are also selective in regard to the portions of the bank they inhabit (Wigley, 1959). Inasmuch as the composition of the bottom sediments on Georges Bank varies from place to place and the geographic distribution of some benthic invertebrates and fishes are closely associated with sediment type, a survey of Georges Bank sediments was undertaken to provide more detailed information on the geographic distribution of the various sediment types. This will provide a basis for future studies concerning the significance of sediments as they affect the occurrence of bottom-dwelling animals.

Specific objectives of this survey were twofold: (1) to ascertain the particle size composition and related components of the sediments, and (2) to make a preliminary quantitative study of the benthic fauna. Only the sediments will be discussed in this report.

Previous Studies

The first observations of Georges Bank sediments were made by the U. S. Coast Survey (Pourtalès, 1869) and the U. S. Fish Commission (Murray, 1885). These findings have been supplemented from time to time and are recorded on standard navigational charts published by the U. S. Coast and

[1] Manuscript received April 11, 1960.

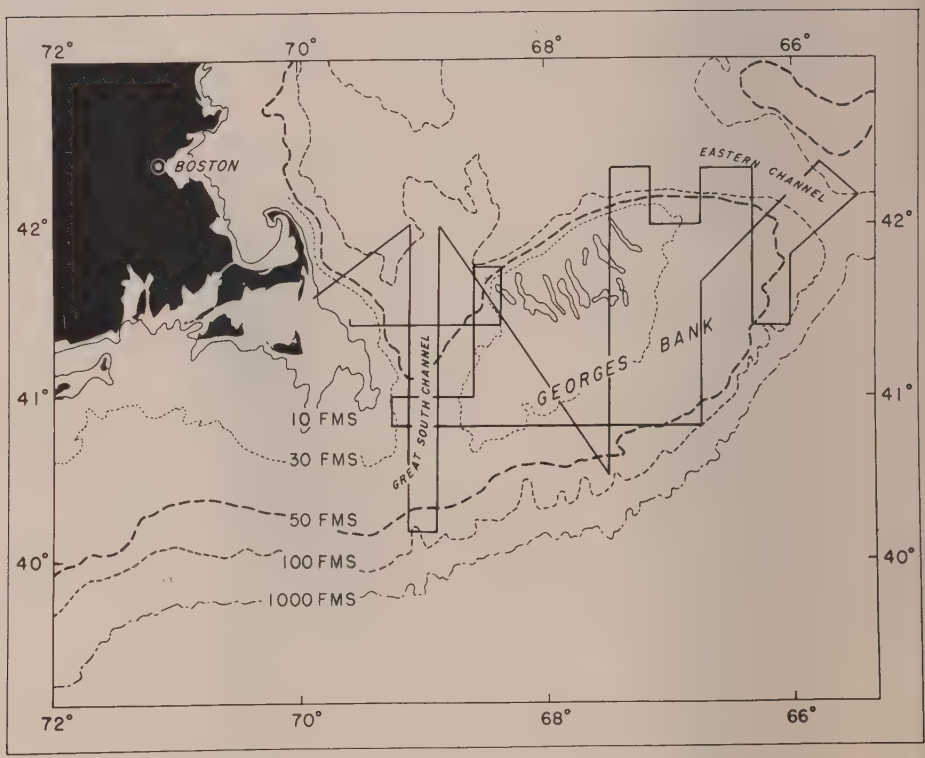

FIG. 1.—Bathymetric chart of Georges Bank with track of sampling stations plotted.

Geodetic Survey. The sediment data plotted on these charts is necessarily inconspicuous. Consequently, for purposes of analysis and study, these charts were reproduced in a more comprehensible format by Shepard (1932). Shepard, Trefethen, and Cohee (1934) refined this sediment chart by incorporating with the old survey data some additional information from various sources. Five years later another revision was published by Shepard (1939). Most of these data, as explained by Shepard (1939), are rather cursory observations of small sediment samples taken by means of sounding leads and small snapper-type samplers. Nevertheless, a check on several hundred samples by Shepard and Cohee (1936) has confirmed the general reliability of these descriptions.

A fairly recent sediment study, using an entirely new set of samples, was conducted by Stetson (1938). His work was based on numerous samples from 13 transects across the continental shelf on the eastern coast of the United States between Maine and Florida. However, only a small section of the area studied by Stetson, a coastal strip east of Cape Cod, coincides with the area included in the present investigation. In this sector he found four sediment zones approximately parallel to the coastline. They occurred in the following order, proceeding seaward from shore: (a) well sorted fine sand, (b) well sorted coarse sand, (c) poorly sorted silt and clay, and (d) well sorted sand.

The U. S. Coast and Geodetic Survey, in collaboration with the Woods Hole Oceanographic Institution, prepared a bottom sediment chart of the Georges Bank region. This chart, U.S.C. & G.S. No. 1107-BS, dated August 1942, was compiled for the National

Defense Research Committee and appears to be based largely on U. S. Coast and Geodetic Survey results, discussed above, and possibly supplemented by other samples.

A special sediment chart of Georges Bank and vicinity was prepared by Colton (1955) for use in connection with a study of the distribution of haddock. For this purpose, sediments were classified into two categories: (1) particle diameters greater than 0.1 mm, and (2) particle diameters mostly less than 0.1 mm. This chart is based on sediment data from U. S. Coast and Geodetic Survey charts 1106A and 1107A, supplemented by more than 250 new bottom samples.

METHODS AND MATERIALS

The samples were collected August 20–30, 1957, aboard the U. S. Fish and Wildlife Service research vessel *Albatross III* at 223 locations spaced at 5-mile intervals along the track shown in figure 1. Most of the traverses cross the bank perpendicular to the depth gradient, and a large proportion of the samples were taken from the bank's perimeter where the sediments were more varied. Sediment samples were collected with a Smith-McIntyre sampler (Smith and McIntyre, 1954). This sampler was selected because of its moderately large capacity, 1/10 m^2, and its reliability in securing a sample under difficult conditions. A secondary factor considered in selecting this sampler was the desirability of obtaining quantitative faunal samples at the same time sediments were collected.

Sediment from the sampler was emptied into a tub. Macroscopic organisms were removed and a 1-quart subsample packed in a cardboard container. Ashore the samples were partially air-dried and sent to the New York Soil Testing Laboratory for analysis.

Mechanical analysis of the sediments was conducted, with slight modification, according to the procedure outlined by Richards (1954). In brief, the analysis was as follows: The sample was air-dried, mixed, and quartered. One quarter was sorted through a graded series of sieving screens with mesh openings of 16, 8, 4, and 2 mm. Material remaining on each screen was weighed and recorded. The mollusk shell fragments in all of these fractions were separated from the inorganic matter and weighed.

A 10-gm sample of sediment composed of fractions less than 2 mm in diameter was treated with hydrogen peroxide to remove the organic matter. This portion of the sample was then water-washed and later oven-dried at 110° C and weighed. A solution of sodium hexametaphosphate was added to the sample, and it was placed in a reciprocating shaker overnight for dispersion. The sample was then washed through a 0.062 mm sieve to separate silts and clays from the sand fractions. After drying, the sands were sorted through a graded series of sieves having mesh openings of 1.0, 0.5, 0.25, and 0.125 mm by agitation in a mechanical shaker for 3 minutes. The weight of each fraction was measured and recorded.

Standard pipetting methods were used in determining the amounts of silt (0.062 −0.004 mm) and clay (<0.004 mm).

Organic content was determined from a portion of the sample not utilized in the particle size analysis. A 2-gm sample composed of particles less than 1 mm in size was subjected to wet combustion of the organic matter using chromic and sulfuric acids according to the modified Walkley procedure described by Peech and others (1947).

Color was determined by comparing the dry sample with Munsell Soil Color Chart.[2]

The six parameters outlined by Inman (1952) for describing the size distribution of sediment components were calculated for each of the samples considered in this study. These parameters: the mean diameter, median diameter, standard deviation, kurtosis, and two measures of skewness, provide data necessary for recalculation of sediment cumulative frequency curves, thus eliminating the need for reporting the complete mechanical analyses. Values for all descriptive measures for each sediment are tabulated either in the text or the appendix. Formulae for all measures used herein may be found in Inman's paper.

In order to facilitate the mathematical computations and comparisons of the various descriptive parameters, the phi (ϕ) notation of Krumbein (1936) is used. Phi, as utilized in this analysis, is the symbol for

[2] Munsell Soil Color Charts, 1954 edition. Munsell Color Company, Inc., 10 East Franklin Street, Baltimore 2, Maryland.

TABLE 1.—*Textural grades and Wentworth classes with corresponding size ranges of each in millimeters and phi units*

Wentworth classes	Grade	Size (mm)	Phi units (ϕ)
	Gravel	32	−5
Coarse pebble		16	−4
Medium pebble		8	−3
Small pebble		4	−2
Granule		2	−1
Very coarse sand	Sand	1	0
Coarse sand		0.5	1
Medium sand		0.25	2
Fine sand		0.125	3
Very fine sand		0.062	4
Silt	Silt	0.004	8
Clay	Clay	<0.004	>8

the negative logarithm to the base 2 of particle diameter in millimeters. A conversion table from millimeters to phi units is included in table 1.

In presenting the data in graphic form, especially in regard to geographic distribution (figs. 1, 2, and 3), it has been necessary in many instances to extrapolate a considerable distance. It should be mentioned that in doing this, previously published data have been used for guidance.

RESULTS

General

The results of this study are in basic agreement with previous investigations outlined above, but many refinements are made and a considerable amount of new information is added. Sediments on Georges Bank and adjacent areas sampled consist chiefly of sands. A large section in the central part of the bank is composed primarily of medium sand—particle diameters between 0.50 and 0.25 mm. A rather broad strip in the southwestern section of the bank and a narrow band along most of the

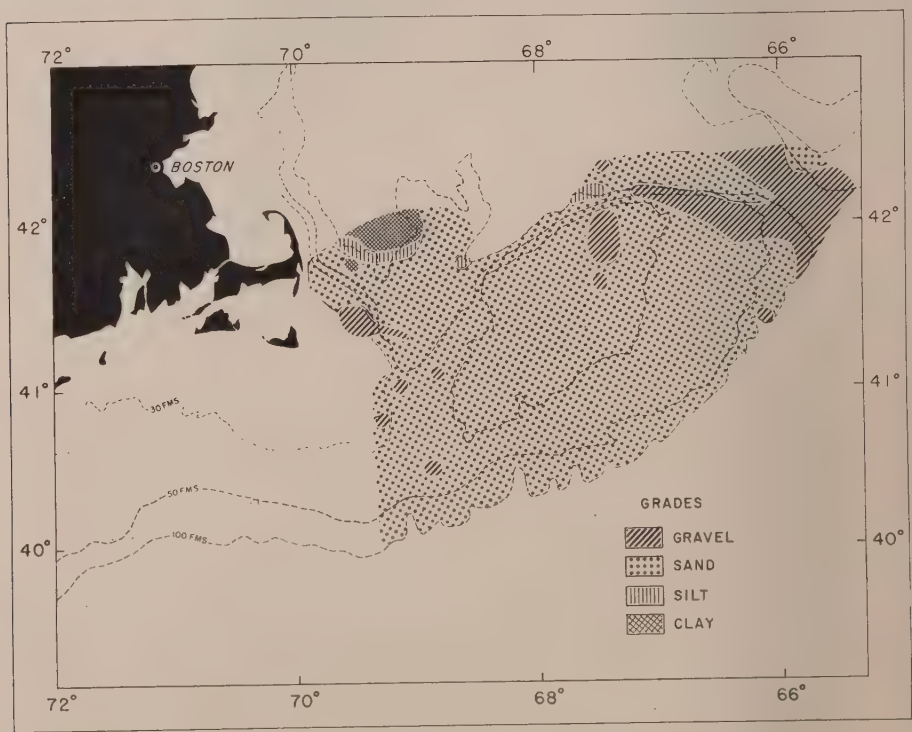

FIG. 2.—Geographic distribution of sediment grades.

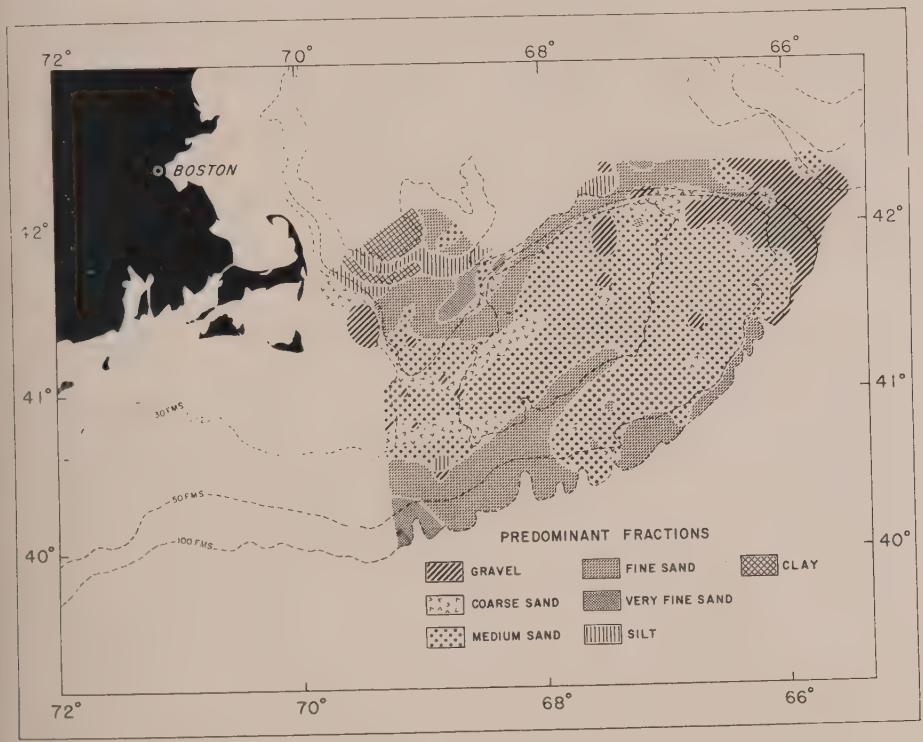

FIG. 3.—Geographic distribution of sediment predominant fractions.

bank's periphery consists mainly of fine sand—0.25 to 0.125 mm. Very fine sands, silts, and clays surround the bank in the deeper water except on the eastern end where gravels predominate.

Table 2 contains the main body of data resulting from this study. Supplementary data which may be used for reference, such as station location, median and mean particle diameter, two measures of size distribution skewness, and kurtosis are listed in the appendix.

Sediment Types

Some of the most useful information resulting from this survey is the delineation of the areal distribution of the various sediment types. Sediments can be classified according to several systems, depending upon the degree of refinement desired. In this report three classifications of sediment type have been selected: (1) grades (2) predominant fractions, and (3) textural classes.

Grades—The first classification of sediment types to be discussed, and the least refined, is a series of only four categories designated as grades. The four grades are: gravel, sand, silt, and clay. Grade designation for each sample is determined by that fraction most abundant in the sample. Size range and name of each grade are included in table 1. The grade of each sample is listed in column 3 of table 2, and the geographic distribution of these grades is illustrated in figure 2.

It is evident from figure 2 that sand is by far the most prevalent grade in this region, comprising more than three-fourths of the entire area. Sand also occurs in the deep water adjacent to the northeastern edge of the bank and is present on the eastern side of the Eastern Channel. Relatively small tracts of silt and clay occur in the deep water area northwest of Georges Bank.

TABLE 2.—*Principal descriptive features of each sediment sample and the water depth at the locality from which they were taken*

Station[1]	Water depth (fms)	Grade	Predominant fraction	Textural class	Median diameter (mm)	Phi deviation measure (ϕ)	Organic content (%)	Shell content (%)	Color
1	15	Sand	Coarse sand	Sand	1.07	0.85	0.1	<1	V. pale brown (S)[2]
2	44	Sand	Coarse sand	Sand	0.90	2.05	0.4	6	Gray brown
3	81	Sand	Silt	Silty sand	0.07	1.75	1.2	0	Lt. brown gray
4	95	Clay	Clay	Silty clay	0.02	1.95	1.2	0	Gray
5	106	Silt	Silt	Clayey silt	0.02	1.80	2.6	0	Gray
6	111	Clay	Clay	Silty clay	0.01	1.15	3.0	0	Gray
7	114	Clay	Clay	Silty clay	0.01	0.90	3.4	0	Gray
8	122	Clay	Clay	Silty clay	0.01	1.15	3.4	0	Gray
9	107	Clay	Clay	Sand-silt-clay	0.04	3.10	2.2	0	Gray
10	106	Clay	Clay	Silty clay	0.02	1.75	3.2	0	Lt. gray brown
11	98	Silt	Silt	Clayey silt	0.02	1.80	2.7	0	Lt. gray brown
12	96	Sand	Clay	Sand-silt-clay	0.06	3.15	1.5	0	Lt. gray brown
13	87	Sand	Fine sand	Sand	0.33	2.15	0.6	0	Lt. gray brown
14	90	Sand	Fine sand	Gravelly sand	0.44	3.15	0.6	0	Gray
15	79	Sand	Medium sand	Sand	0.50	0.80	0.4	0	Lt. brown gray
16	86	Sand	Medium sand	Gravelly sand	1.15	2.55	0.4	<1	Lt. brown gray
17	90	Gravel	Gravel	Sandy gravel	4.20	2.75	0.3	1	Lt. brown gray
18	83	Sand	Medium sand	Gravelly sand	0.66	2.15	0.6	<1	Gray brown
19	66	Sand	Medium sand	Gravelly sand	1.25	1.95	<0.1	2	Pale brown (S)
20	45	Sand	Coarse sand	Sand	0.72	0.35	0.1	<1	V. pale brown (S)
21	42	Sand	Medium sand	Gravelly sand	0.54	2.10	0.1	<1	Lt. yellowish brown (S)
22	41	Sand	Medium sand	Gravelly sand	2.30	2.85	0.1	1	Lt. brown gray (S)
23	37	Gravel	Gravel	Sandy gravel	5.65	2.95	0.2	1	Gray brown (S)
24	42	Sand	Coarse sand	Gravelly sand	1.07	1.70	<0.1	4	Pale brown (S)
25	40	Sand	Medium sand	Sand	0.62	1.90	0.1	1	V. pale brown (S)
26	38	Sand	Fine sand	Sand	0.36	0.50	0.2	<1	V. pale brown (S)
27	43	Sand	Fine sand	Sand	0.19	0.15	0.6	0	Gray brown
28	46	Sand	Fine sand	Sand	0.18	0.40	0.7	0	Lt. brown gray
29	48	Sand	Very fine sand	Sand	0.16	0.50	0.7	0	Gray brown
30	52	Sand	Very fine sand	Sand	0.15	0.55	0.6	1	Gray brown
31	58	Sand	Very fine sand	Sand	0.22	1.60	0.6	3	Gray brown
32	74	Sand	Very fine sand	Sand	0.17	1.20	0.6	1	Gray brown
33	83	Sand	Fine sand	Sand	0.24	0.65	0.6	0	Lt. brown gray
34	60	Sand	Fine sand	Sand	0.29	1.05	0.4	1	Lt. brown gray
35	49	Sand	Fine sand	Sand	0.27	0.90	0.4	4	Lt. gray brown
36	44	Sand	Fine sand	Sand	0.21	0.30	0.4	1	Lt. brown gray
37	39	Gravel	Gravel	Gravel	22.75	0.00	0.1	8	Light gray (S)
38	37	Sand	Silt	Silty sand	0.22	1.95	0.2	4	Light gray (S)
39	34	Sand	Medium sand	Sand	0.66	1.90	0.1	<1	V. pale brown (S)
40	33	Sand	Medium sand	Sand	0.72	1.90	0.1	2	V. pale brown (S)
41	35	Sand	Medium sand	Gravelly sand	0.54	2.55	0.1	<1	V. pale brown (S)
42	37	Sand	Medium sand	Sand	0.66	0.45	0.2	0	V. pale brown (S)
43	34	Sand	Medium sand	Sand	0.72	1.10	0.1	0	V. pale brown (S)
44	35	Gravel	Gravel	Gravel	11.40	1.05	<0.1	2	Pale brown (S)
45	45	Sand	Medium sand	Sand	0.41	1.30	0.2	8	Lt. brown gray (S)
46	51	Sand	Medium sand	Sand	0.44	1.60	0.1	<1	Lt. brown gray (S)
47	61	Sand	Fine sand	Sand	0.29	1.15	0.3	8	Lt. olive brown (S)
48	73	Sand	Fine sand	Sand	0.22	0.50	0.5	<1	Gray brown
49	80	Sand	Very fine sand	Sand	0.17	1.45	<0.1	0	Gray brown
50	85	Sand	Very fine sand	Silty sand	0.11	1.40	1.0	0	Gray brown
51	82	Sand	Fine sand	Gravelly sand	0.19	2.70	0.9	0	Gray brown
52	90	Sand	Silt	Sand-silt-clay	0.08	3.25	1.8	<1	Lt. olive gray
53	87	Sand	Silt	Sand-silt-clay	0.25	3.65	1.7	0	Gray brown
54	74	Sand	Medium sand	Sand	0.66	1.35	0.7	0	Olive gray
55	76	Sand	Fine sand	Sand	0.41	1.60	0.6	0	Gray brown
56	84	Sand	Medium sand	Gravelly sand	0.66	2.70	0.8	0	Gray brown
57	84	Sand	Fine sand	Silty sand	0.25	2.85	1.3	0	Lt. brown gray
58	92	Silt	Silt	Clayey silt	0.12	0.65	3.3	0	Lt. olive gray
59	99	Sand	Very fine sand	Silty sand	0.08	1.25	1.9	0	Lt. olive gray
60	93	Sand	Medium sand	Sand	0.38	2.20	0.9	0	Gray brown
61	27	Sand	Coarse sand	Gravelly sand	0.82	1.85	0.1	<1	Pale olive (S)
62	25	Sand	Fine sand	Sand	0.46	2.25	0.2	<1	Pale yellow (S)
63	26	Sand	Fine sand	Sand	0.36	0.20	0.3	<1	Light gray (S)
64	24	Sand	Coarse sand	Sand	1.00	0.45	<0.1	0	V. pale brown (S)
65	17	Sand	Coarse sand	Sand	1.32	0.25	<0.1	<1	V. pale brown (S)
66	16	Sand	Medium sand	Sand	0.54	0.55	0.1	<1	White (S)
67	23	Sand	Medium sand	Sand	0.66	0.40	0.1	<1	Light gray (S)
68	24	Sand	Medium sand	Sand	0.36	0.10	0.1	<1	White (S)
69	27	Sand	Fine sand	Sand	0.27	0.30	0.2	2	White (S)
70	28	Sand	Fine sand	Sand	0.25	0.30	0.2	0	Light gray (S)
71	33	Sand	Medium sand	Sand	0.58	0.85	0.2	0	Pale yellow (S)
72	36	Sand	Medium sand	Sand	0.50	0.55	0.2	2	Lt. yellowish brown (S)
73	38	Sand	Medium sand	Sand	0.50	0.75	0.2	8	Lt. yellowish brown (S)
74	44	Sand	Fine sand	Sand	0.24	0.85	0.4	3	Pale olive
75	51	Sand	Medium sand	Sand	0.50	0.55	0.2	2	Pale yellow (S)
76	66	Sand	Medium sand	Sand	0.50	0.95	0.2	2	Pale yellow (S)
78	64	Sand	Medium sand	Sand	0.38	0.80	0.2	1	Pale yellow (S)

[1] Station is synonymus with sample number.
[2] (S) is an abbreviation for speckled, V.—Very, Lt.—Light, and Dk.—Dark.

TABLE 2.—*Continued*

Station[1]	Water depth (fms)	Grade	Predominant fraction	Textural class	Median diameter (mm)	Phi deviation measure (φ)	Organic content (%)	Shell content (%)	Color
79	47	Sand	Coarse sand	Sand	0.82	0.65	0.2	1	Lt. yellowish brown (S)
80	46	Sand	Medium sand	Sand	0.38	0.85	0.2	8	Pale olive (S)
81	44	Sand	Medium sand	Sand	0.38	0.80	0.2	8	Pale yellow (S)
82	42	Sand	Fine sand	Sand	0.31	0.65	0.4	11	Pale yellow (S)
83	37	Sand	Medium sand	Sand	0.36	0.55	0.2	6	Pale yellow (S)
84	33	Sand	Medium sand	Sand	0.38	0.55	0.2	0	Pale yellow (S)
85	30	Sand	Fine sand	Sand	0.27	0.40	0.2	0	Light gray (S)
86	24	Sand	Fine sand	Sand	0.36	0.35	0.2	1	White (S)
87	16	Sand	Medium sand	Sand	0.72	0.80	0.2	5	White (S)
88	18	Sand	Medium sand	Sand	0.46	0.50	0.2	2	Pale yellow (S)
89	27	Sand	Medium sand	Sand	0.50	0.45	0.1	1	Pale yellow (S)
90	23	Sand	Coarse sand	Sand	0.82	0.80	0.2	1	Pale yellow (S)
91	27	Gravel	Gravel	Sandy gravel	18.50	2.70	<0.1	6	Light gray (S)
92	18	Sand	Medium sand	Gravelly sand	1.42	2.00	0.1	2	Light gray (S)
93	29	Gravel	Gravel	Gravel	13.00	2.35	<0.1	1	Pale olive (S)
94	25	Gravel	Gravel	Sandy gravel	5.25	2.40	0.1	<1	Pale yellow (S)
95	25	Gravel	Gravel	Sandy gravel	10.50	2.50	<0.1	1	Pale yellow (S)
96	44	Sand	Medium sand	Sand	0.66	1.90	0.1	6	Pale yellow (S)
97	85	Sand	Fine sand	Sand	0.21	0.75	0.9	0	Olive gray
98	126	Silt	Silt	Sandy silt	0.07	1.65	2.3	0	Olive gray
99	151	Sand	Fine sand	Sand	0.27	2.25	0.9	0	Gray brown
100	158	Gravel	Gravel	Sandy gravel	13.00	3.20	0.3	0	Lt. brown gray
101	144	Sand	Fine sand	Gravelly sand	0.31	2.85	0.5	0	Lt. olive gray
102	128	Sand	Very fine sand	Silty sand	0.18	2.45	0.8	0	Lt. olive gray
103	92	Sand	Fine sand	Sand	0.25	0.50	0.3	0	Lt. olive gray (S)
104	34	Gravel	Gravel	Sandy gravel	15.00	2.65	0.1	17	Lt. olive gray (S)
105	32	Sand	Coarse sand	Sand	1.32	1.10	<0.1	5	Light gray (S)
106	26	Sand	Coarse sand	Gravelly sand	2.00	1.70	<0.1	<1	Light gray (S)
107	30	Sand	Fine sand	Sand	0.18	0.05	0.1	0	Olive (S)
108	32	Sand	Medium sand	Sand	0.46	0.20	<0.1	0	White (S)
109	35	Sand	Medium sand	Sand	0.66	0.20	<0.1	0	Light gray (S)
110	40	Sand	Coarse sand	Sand	0.90	0.45	<0.1	9	White (S)
111	40	Sand	Medium sand	Gravelly sand	1.75	2.00	<0.1	2	Light gray (S)
112	39	Gravel	Gravel	Gravel	13.00	2.30	<0.1	1	Pale brown (S)
113	39	Gravel	Gravel	Gravel	22.75	0.00	<0.1	7	——
114	88	Sand	Coarse sand	Sand	0.75	1.05	<0.1	1	V. pale brown (S)
115	152	Sand	Fine sand	Sand	0.19	1.30	0.5	0	Lt. olive gray
116	182	Sand	Fine sand	Gravelly sand	0.33	2.40	0.5	0	Gray brown
117	191	Sand	Fine sand	Sand	0.29	1.65	0.3	0	Gray brown
118	172	Sand	Medium sand	Gravelly sand	1.75	3.05	0.1	0	Olive gray
119	156	Gravel	Gravel	Sandy gravel	4.27	2.85	0.1	0	Olive gray (S)
120	141	Gravel	Gravel	Gravel	22.75	1.15	<0.1	0	Gray brown (S)
121	121	Sand	Medium sand	Gravelly sand	0.72	2.30	0.1	0	Lt. brown gray (S)
122	105	Sand	Fine sand	Gravelly sand	0.62	2.20	<0.1	0	Gray brown (S)
123	58	Sand	Gravel	Gravelly sand	1.24	2.70	<0.1	2	Light gray (S)
124	47	Gravel	Gravel	Gravel	8.00	2.10	<0.1	1	Light gray (S)
125	46	Gravel	Gravel	Gravel	22.75	1.55	0.1	9	Light gray (S)
126	44	Gravel	Gravel	Gravel	9.20	2.00	0.1	3	Light gray (S)
127	43	Sand	Coarse sand	Sand	0.94	1.15	<0.1	15	Lt. brown gray (S)
128	43	Sand	Medium sand	Sand	0.62	0.40	<0.1	2	V. pale brown (S)
129	47	Sand	Medium sand	Sand	0.66	0.75	0.1	14	V. pale brown (S)
130	48	Sand	Medium sand	Sand	0.72	0.65	0.2	10	Pale brown (S)
131	50	Sand	Medium sand	Sand	0.90	1.70	0.1	5	Light gray (S)
132	61	Sand	Medium sand	Sand	0.72	1.65	<0.1	9	Light gray (S)
133	67	Sand	Fine sand	Sand	0.31	0.90	<0.1	8	Light gray (S)
134	76	Gravel	Gravel	Sandy gravel	3.00	2.85	0.1	3	Lt. brown gray (S)
135	130	Sand	Gravel	Gravelly sand	2.45	2.05	<0.1	<1	Light gray (S)
136	79	Sand	Medium sand	Gravelly sand	0.94	1.75	0.2	1	Lt. brown gray (S)
137	58	Sand	Medium sand	Sand	0.66	0.60	<0.1	1	Light gray (S)
138	52	Sand	Medium sand	Gravelly sand	0.90	1.40	<0.1	8	Lt. brown gray (S)
139	54	Sand	Medium sand	Sand	0.66	0.40	0.1	2	Light gray (S)
140	50	Sand	Gravel	Gravelly sand	1.62	1.65	<0.1	6	Pale brown (S)
141	59	Gravel	Gravel	Sandy gravel	4.57	2.50	<0.1	2	Lt. brown gray (S)
142	102	Gravel	Gravel	Gravel	22.75	1.00	<0.1	0	Lt. brown gray (S)
144	134	Gravel	Gravel	Gravel	22.75	0.40	<0.1	<1	——
146	75	Gravel	Gravel	Sandy gravel	8.00	2.40	<0.1	<1	Lt. brown gray (S)
148	60	Gravel	Gravel	Gravel	18.50	2.40	<0.1	3	Lt. brown gray (S)
149	76	Sand	Medium sand	Gravelly sand	0.72	3.00	0.1	3	Lt. brown gray (S)
150	83	Sand	Medium sand	Gravelly sand	0.90	1.80	0.1	<1	Lt. brown gray (S)
151	126	Sand	Coarse sand	Gravelly sand	1.75	1.45	0.1	0	Gray brown (S)
152	130	Gravel	Gravel	Sandy gravel	3.72	1.95	<0.1	0	Gray brown (S)
153	129	Gravel	Gravel	Gravel	22.75	0.00	<0.1	0	——
154	110	Sand	Coarse sand	Sand	0.72	0.30	0.1	<1	Light gray (S)
156	44	Gravel	Gravel	Gravel	11.40	1.45	<0.1	<1	Brown (S)
157	43	Gravel	Gravel	Gravel	18.50	1.05	0.1	3	Pale yellow (S)
158	45	Sank	Medium sand	Gravelly sand	2.00	2.30	0.1	10	Light gray (S)
159	43	Sand	Medium sand	Sand	0.66	0.65	0.1	14	V. pale brown (S)
160	40	Sand	Medium sand	Gravelly sand	1.54	2.90	<0.1	18	White (S)
161	36	Sand	Medium sand	Sand	0.66	1.15	0.1	7	White (S)
162	38	Sand	Medium sand	Sand	0.38	0.50	0.1	2	Light gray (S)

(*Table 2 continud on following page*)

TABLE 2.—*Continued*

Station[1]	Water depth (fms)	Grade	Predominant fraction	Textural class	Median diameter (mm)	Phi deviation measure (φ)	Organic content (%)	Shell content (%)	Color
163	39	Sand	Medium sand	Sand	0.41	0.50	0.1	4	Light gray (S)
164	38	Sand	Medium sand	Sand	0.44	0.35	0.1	0	Light gray (S)
165	43	Sand	Gravel	Gravelly sand	1.24	3.05	0.1	9	Light gray (S)
166	42	Sand	Medium sand	Sand	0.72	0.55	0.1	<1	V. pale brown (S)
167	44	Sand	Medium sand	Sand	0.54	0.45	0.1	12	Light gray (S)
168	42	Sand	Coarse sand	Sand	0.76	0.60	0.1	6	V. pale brown (S)
169	47	Sand	Medium sand	Sand	0.62	0.50	0.1	3	Light gray (S)
170	49	Sand	Medium sand	Sand	0.38	0.35	0.2	17	Pale olive (S)
171	56	Sand	Fine sand	Sand	0.36	0.40	0.2	25	Pale olive (S)
172	133	Sand	Fine sand	Sand	0.21	0.60	0.5	0	Lt. olive gray (S)
173	62	Sand	Medium sand	Sand	0.58	0.55	0.1	7	Light gray (S)
174	56	Sand	Fine sand	Sand	0.28	0.45	0.3	9	Pale olive (S)
175	52	Sand	Fine sand	Sand	0.31	0.55	0.2	4	Pale olive (S)
176	52	Sand	Fine sand	Sand	0.25	0.50	0.4	2	Lt. olive gray (S)
177	50	Sand	Fine sand	Sand	0.22	0.70	p.3	16	Pale olive (S)
178	46	Sand	Medium sand	Sand	0.36	0.80	0.3	7	Pale olive (S)
179	44	Sand	Medium sand	Sand	0.36	0.85	0.2	13	Lt. olive gray (S)
180	41	Sand	Medium sand	Sand	0.66	0.70	0.2	0	Pale olive (S)
181	37	Sand	Coarse sand	Sand	0.94	1.20	0.1	2	V. pale brown (S)
182	38	Sand	Medium sand	Sand	0.41	0.45	0.1	0	Pale yellow (S)
183	38	Sand	Fine sand	Sand	0.29	0.45	0.3	9	Pale olive (S)
184	36	Sand	Fine sand	Sand	0.29	0.55	0.2	<1	Pale yellow (S)
185	32	Sand	Fine sand	Sand	0.27	0.25	0.2	<1	Light gray (S)
186	31	Sand	Fine sand	Sand	0.33	0.30	0.1	2	White (S)
187	25	Sand	Coarse sand	Sand	0.80	0.40	0.4	0	Light gray (S)
188	29	Sank	Medium sand	Sand	0.50	0.50	0.1	<1	Light gray (S)
189	34	Sand	Coarse sand	Gravelly sand	1.15	1.55	0.1	1	Light gray (S)
190	36	Sand	Coarse sand	Sand	0.72	0.90	0.1	0	V. pale brown (S)
191	36	Sand	Medium sand	Gravelly sand	0.62	2.40	0.1	<1	Light gray (S)
192	42	Sand	Medium sand	Sand	0.46	0.60	0.2	15	Light gray (S)
193	36	Sand	Coarse sand	Sand	1.00	0.80	0.1	1	Light gray (S)
194	34	Sand	Medium sand	Gravelly sand	1.00	2.10	<0.1	6	Light gray (S)
195	28	Gravel	Gravel	Sandy gravel	18.50	2.45	<0.1	1	Light gray (S)
196	35	Sand	Medium sand	Gravelly sand	0.62	2.45	0.1	1	Light gray (S)
197	37	Sand	Medium sand	Gravelly sand	1.32	2.55	0.1	4	Lt. brown gray (S)
198	33	Sand	Medium sand	Gravelly sand	1.32	2.10	0.2	2	Gray brown
199	36	Gravel	Gravel	Sandy gravel	12.25	2.90	0.1	8	Gray brown
200	43	Sand	Medium sand	Gravelly sand	0.82	2.20	0.1	1	Lt. brown gray
201	42	Sand	Medium sand	Gravelly sand	1.32	2.50	0.1	<1	Lt. brown gray
202	36	Sand	Coarse sand	Sand	0.82	0.75	0.1	<1	Pale yellow
203	35	Gravel	Gravel	Sandy gravel	5.65	2.25	<0.1	<1	Lt. brown gray
204	25	Sand	Medium sand	Gravelly sand	1.32	1.85	<0.1	2	Lt. yellowish brown
205	31	Sand	Medium sand	Gravelly sand	1.00	2.35	0.1	<1	Lt. yellowish brown
206	31	Sand	Coarse sand	Gravelly sand	1.50	1.90	<0.1	<1	Lt. brown gray
207	34	Sand	Medium sand	Gravelly sand	0.44	2.20	0.1	0	Lt. brown gray
208	37	Sand	Fine sand	Sand	0.21	0.60	0.8	0	Gray brown
209	47	Sand	Fine sand	Sand	0.18	0.55	0.6	<1	Lt. olive brown
210	56	Sand	Coarse sand	Sand	0.66	1.70	2.5	2	Lt. yellowish brown
211	72	Sand	Very fine sand	Gravelly sand	0.58	2.85	1.0	0	Gray brown
213	102	Sand	Very fine sand	Clayey sand	0.24	2.20	1.3	0	Gray brown
214	105	Sand	Medium sand	Gravelly sand	0.58	2.65	1.1	<1	Dk. gray brown
215	90	Sand	Very fine sand	Sand	0.12	2.35	1.6	0	Gray brown
216	12	Sand	Coarse sand	Sand	0.76	0.60	0.1	0	Lt. brown gray
217	34	Sand	Fine sand	Gravelly sand	1.42	2.65	0.1	2	Pale olive
218	42	Sand	Fine sand	Sand	0.29	0.45	0.4	<1	Olive gray
219	44	Sand	Fine sand	Sand	0.22	0.60	0.4	<1	Olive gray
220	52	Sand	Fine sand	Sand	0.19	0.50	0.4	<1	Olive gray
221	64	Sand	Fine sand	Sand	0.29	0.70	0.2	1	Olive gray
222	79	Sand	Fine sand	Gravelly sand	0.36	2.20	0.4	1	Olive gray
223	84	Sand	Fine sand	Sand	0.36	1.70	0.5	<1	Dk. gray brown
224	89	Sand	Fine sand	Sand	0.44	1.85	0.3	<1	Gray brown
225	86	Sand	Fine sand	Gravelly sand	0.82	2.40	0.1	1	Brown
226	62	Sand	Fine sand	Sand	0.44	1.55	0.2	13	Brown
227	22	Gravel	Gravel	Gravel	8.60	2.00	<0.1	4	Gray brown
228	18	Gravel	Gravel	Gravel	22.75	0.00	<0.1	6	Lt. yellowish brown
229	16	Gravel	Gravel	Sandy gravel	9.20	2.40	<0.1	1	Light gray

Generally the clays are found in the deepest part of this basin and silts in slightly shallower depths. Gravels are encountered in small patches in the shallower sections of Great South Channel and on the north-central part of the bank. The largest expanse of gravel is found on the northeastern end of the bank. In this area a band of gravel extends along the northeast perimeter out to the bank's eastern end and throughout most of Eastern Channel to the southwestern corner of Browns Bank.

Predominant Fractions—The second classification of sediment types to be considered, and intermediate in degree of refinement, is a group of categories termed predominant

fractions. The particle-size category constituting the largest portion of the sediment sample is designated as the predominant fraction. With the exception of gravels, Wentworth size classes listed in table 1 are utilized for this classification; gravels have been grouped together because of the small number of samples representing most classes of gravels. In column 4 of table 2 is listed the predominant fraction of each sediment sample. The geographic distribution of these fractions is illustrated in figure 3.

The geographic pattern of predominant fractions is similar to that of grades. With relatively few exceptions the sediments in Great South Channel and over most of Georges Bank were predominantly sand fractions. Silt and clay fractions occurred only in the deep-water area northwest of the bank. Comparatively small patches of gravel were found in the central and western part of Great South Channel and along the northern and northeastern edges of Georges Bank.

The predominant fraction having widest distribution in the study area is medium sand (0.25–0.50 mm). This occurred over broad expanses of Georges Bank and covered an exceptionally large portion of the bank, especially in the shallower sections. Fine sand (0.125–0.25 mm) was common along the bank's periphery except on the eastern end. In addition, a tongue of fine sand extended northward onto the bank from the southern edge. Very fine sand (0.062–0.125 mm) was encountered in relatively small areas in three localities: southeastern Great South Channel, northwestern Great South Channel, and at one station in the deep water along the bank's northern edge. Coarse sand (0.5–1.0 mm) was moderately common, especially in relatively shallow water. It occurred in rather narrow strips and small pockets in Great South Channel and along the bank's perimeter.

Clay fractions predominated in the central portion of the deep water basin northwest of Georges Bank. Water depths in this vicinity ranged from approximately 100 to 120 fathoms. Also, in somewhat shallower water, a narrow band of clay was found close to the basin but was separated from the main tract of clay by a band of silt. Silt fractions were most common in this deep water section northwest of the bank, usually adjacent to, or close by, the clay fractions. In addition to its occurrence in this area, silt fractions predominated at two other localities. Two very small pockets of silt were found, one on the southern part of Great South Channel, and the other on the north-central perimeter of the bank.

Textural Classes—The third level of classification of sediment types discussed in this report, and the most refined of the three, is termed textural classes. This is essentially a modification of the first classification (Grades). The most abundant grade, based on weight, is complemented by the second ranking grade, and the result is a binary term expressing the two major constituents of each sediment. An exception to this rule is when one grade makes up 75 percent or more of any one sample. In such instances the term is limited to a single grade. Among the samples analyzed, gravel and sand are the only two classes that fall in this category. In cases where three grades each provide 20 percent or more of the entire sample, all three grades are identified in the textural class terms. Sand-silt-clay is the only representative of this type of textural class encountered in this study. This procedure is in accordance with the system devised by Shepard (1953). The textural class of each sediment is listed in column 5 of table 2; the geographic distribution is illustrated in figure 4.

Undoubtedly the most striking feature of the textural class distribution is the predominance of sand over a large portion of Georges Bank and adjacent areas. The sediments of the entire southern and central parts of the bank, plus large sections in Great South Channel and the northern portion of Georges Bank, come under the textural-class category of sand. As previously stated, a sediment must consist of 75 percent or more of sand to be included in this class.

A second major feature shown in figure 4 is the rather extensive areas where gravels and mixtures of sand and gravel predominate. Gravels are widely distributed over the northeast end of Georges Bank and in Eastern Channel. This large gravel area is nearly surrounded by sandy gravel or gravelly sand sediments, the latter occurring

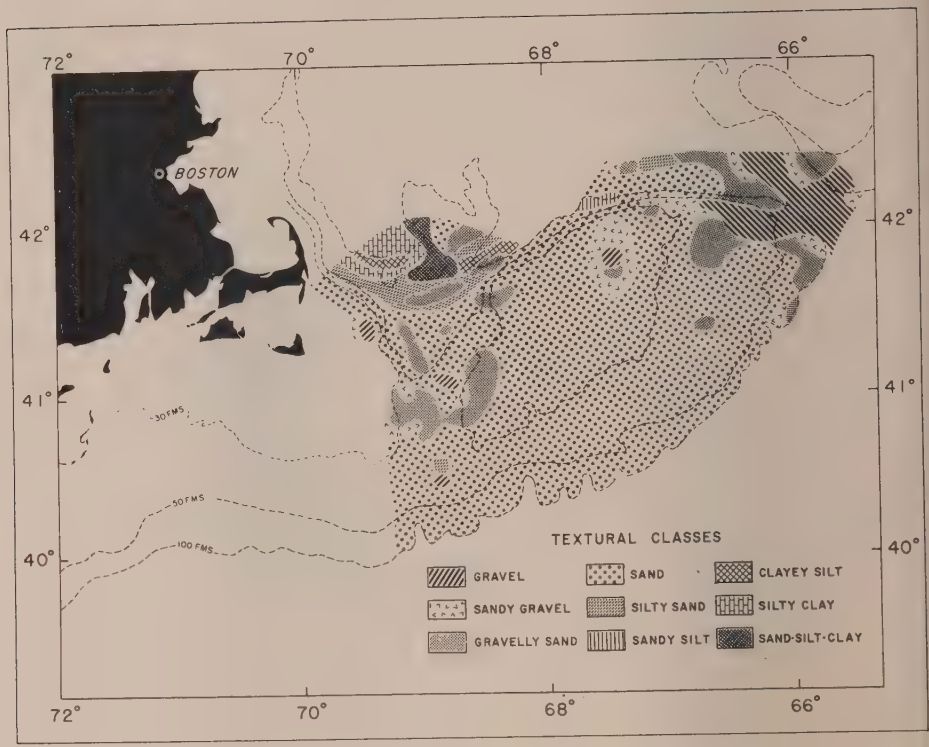

FIG. 4.—Geographic distribution of sediment textural classes.

over a much larger area than the former. Small tracts of gravel occur in Great South Channel and in the north-central part of the bank. Sandy gravel sediments in areas other than those just mentioned are relatively uncommon. Only small tracts are found in Great South Channel and the north-central part of the bank. Gravelly sand sediments occur over rather large areas throughout central and northern Great South Channel, in addition to its occurrence on the bank's eastern end.

Silts and clays and mixtures thereof abound only in the deep-water sector northwest of Georges Bank. Silty clay occurs in the deepest part of the basin and clayey silts are common in slightly shoaler water. In this same vicinity, adjacent to the eastern boundary of the silty clay sediments, is a moderately large tract of sand-silt-clay. This is the only occurrence of this textural class. East of this tract is a variety of textural classes, each covering a rather small area. These sediments are: sand, gravelly sand, silty sand, and clayey silt.

Median Diameter

Sediment median diameter is the midpoint in the size distribution of a sediment sample. Half the sample weight is composed of fractions larger than the median and half of smaller fractions. The median is a more useful measure of central tendency than the mean; since it is closer to the modal diameter, it is less affected by extreme values of skewness. For each sample, two values of median diameter were computed; one in millimeter units, the other in phi (ϕ) units. These are listed in column 6 in table 2 and column 5 in the appendix, respectively, and their geographic distribution is illustrated in figure 5. The mean values are recorded in the appendix.

The median diameters range from 0.0

mm to 22.75 mm. The small values represent samples taken at stations 6, 7, 8, 10, and 11, primarily silt-clay sediments from the deep-water area northwest of Georges Bank. The high values represent samples composed largely of gravels from Eastern Channel and scattered localities in Great South Channel. In addition, a few samples with rather high median diameters were taken from north-central Georges Bank and along the northern and northeastern parts of the bank. By far the largest part of the study area is composed of sediments whose median diameters are intermediate—between 0.25 mm and 1.0 mm.

Geographically, the greatest variation in median values occurs in the vicinity of the bank's perimeter and in the deep water beyond. This suggests that sediment median diameter may be associated with depth. Further inquiry into this aspect has revealed that sediments from the western section of the study area exhibit a distinct trend of decreasing diameter as water depth increases (see figure 6). Pebbles and sands abound in the shallower waters, whereas silts and clays predominate in the deep water. However, this relationship does not apply to the sediments on eastern Georges Bank. There, pebbles and sands are the main constituents in both the shallow- and deep-water samples. Thus the median diameters of these eastern sediments are obviously not well correlated with water depth.

In general, the median particle size of a sediment may be considered indicative of the relative current velocity at the site of deposition, regardless of depth. In many instances the samples from Georges Bank and vicinity with large median diameters were taken at localities where water currents are thought to be strong. Lack of water velocity measurements prohibits detailed analysis of this aspect but, because of its

FIG. 5.—Geographic distribution of sediment median diameters. Values are given in millimeters.

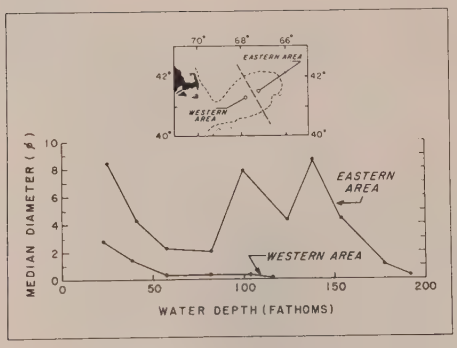

FIG. 6.—The relationship of sediment median diameter to water depth for two groups of samples: (1) eastern area, and (2) western area.

importance, a brief discussion is warranted.

Two east-west transects across Great South Channel will serve to illustrate some relationships between water depth and current velocity with sediment median diameter. The first transect, A–B in figure 7, includes stations 1 through 9. This is a series of samples taken near the coast east of Cape Cod, Massachusetts, nearly perpendicular to the gradient. Water depth at A is 15 fathoms and deepens to 122 fathoms near B and then shoals slightly to 107 fathoms at B (see figure 7). The sediment median diameter at A is 1.07 mm and decreases to 0.01 mm as B is approached, except for the increase to 0.04 mm at B. Thus, in this series the median diameter decreases as depth increases.

Another transect across Great South Channel, C–D in figure 7, reveals a distinctly different relationship between water depth and median diameter from that found at A–B. The water is relatively shallow at each end of transect C–D, 16 and 44 fathoms respectively, and is rather deep, 89 fathoms, at the center. However, the median diameter at C is large, 9.20 mm, and decreases to 0.22 mm at D. Thus the median diameter of the sediments in this area is not related to water depth. An explanation of differences in sediments taken along these two transects is provided by a study of the water currents.

In a comprehensive study of the hydrography of the Gulf of Maine, Bigelow (1927) ascertained that one exit by which water flows out of the Gulf of Maine is along the western side of Great South Channel. Another current he discusses, which is pertinent to this study, is that which flows eastward out of Nantucket Sound and subsequently turns southerly to pass across Nantucket Shoals or down through Great South Channel. Thus the existence of strong currents at A and C accounts for the large-sized sediments there, and weak currents at B and D explain the presence of fine sediments in those areas. The relationships between median diameter and degree of sorting and organic content are discussed in the following sections of this report.

Sorting

The dispersion or dimensional spread of particle sizes on either side of the mean is called sorting. The coefficient of sorting is a measure of the degree of dispersion or, as calculated in phi units, is the phi deviation measure. In column 7 of table 2 the phi deviation measure is listed for each sample, and in figure 8 the geographic distribution of these values is illustrated.

Phi deviations are utilized as an index of turbulence and variations in the velocity of water currents that transport sediments. Poorly sorted sediments, those possessing a

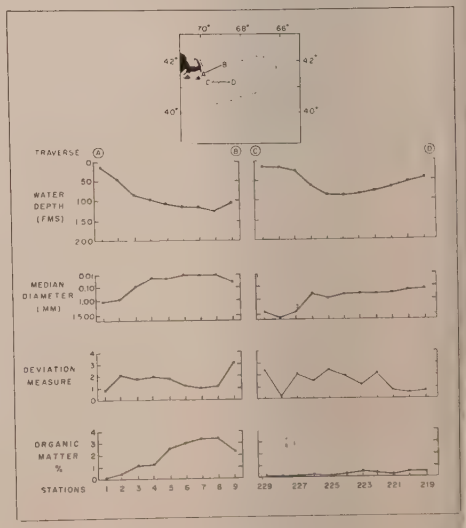

FIG. 7.—Profiles of water depth, median diameter, phi deviation measure, and organic matter at transects A–B and C–D across Great South Channel.

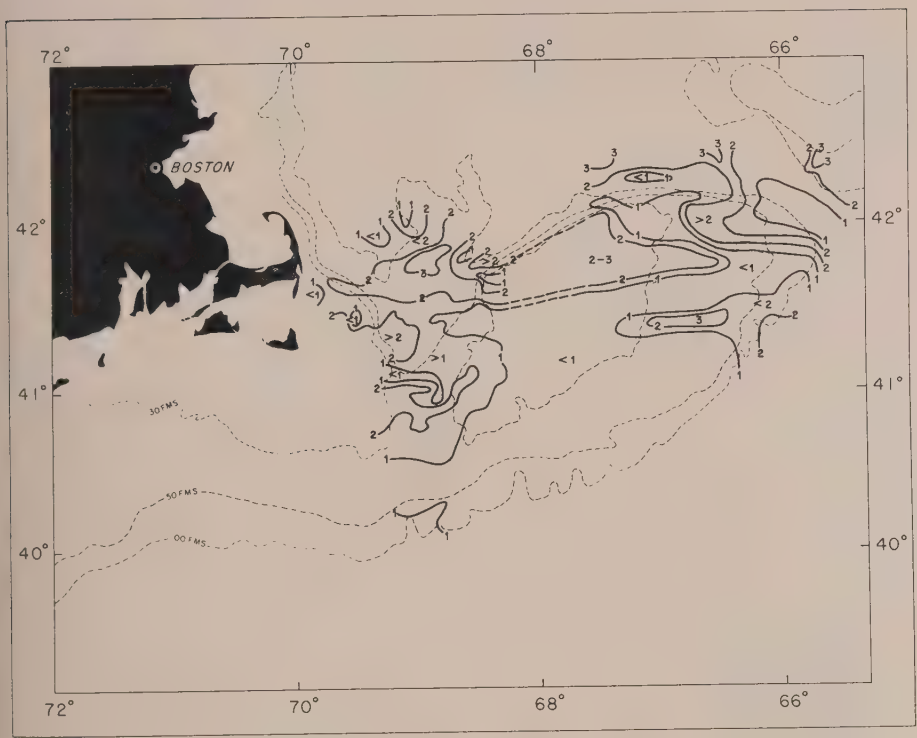

FIG. 8.—Geographic distribution of sediment phi deviation measure (sorting).

wide range in particle sizes, indicate a variable or turbulent current during deposition. Well sorted sediments are an indication of smooth, stable currents.

Georges Bank sediments range from perfectly sorted (0 phi deviation) to very poorly sorted (4.5 phi deviation). A large section in the central and southern parts of the bank contains sediments that are well sorted, having phi deviations of 1.0 or less. Much of this area has sediments that are very well sorted, having phi deviations of 0.5 or less. Small sections along the northern part of the bank and in both channels also have well sorted sediments. Poorly sorted sediments occur chiefly in the channel areas and along the bank's northern edge. It is of interest to note that some of the predominantly fine sediments in the deep-water area northwest of Georges Bank are poorly sorted as are many of the coarse sediments in the channel areas.

Since the phi deviation measure is an index of turbulence or variation in current velocities, the following inferences are drawn: (1) Turbulent and/or variable currents occur in Great South Channel, along much of northern Georges Bank, and in the eastern half of Eastern Channel. (2) Relatively steady and uniform currents prevail over the central and southern parts of Georges Bank.

In areas where the surface- or mid-water currents strike the sea bed, turbulence and/or variations in current velocity are greatest. This is noticeably so in the shallowest section of Great South Channel, in the shoaling area north of Great South Channel, and in the shallows of north-central and northeastern parts of Georges Bank. Also, of particular interest, are indications of a turbulent or variable current flowing westward in the vicinity of Corsair Canyon (41°25′ N., 66°10′ W.).

Phi deviation is not closely associated with water depth, median diameter, or

organic content. See figure 7 for a few illustrations. There is a trend for shallow water sediments to be better sorted than those from deep water, all samples considered. This relationship does not, however, hold for all sections of the study area.

Organic Content

Organic content of Georges Bank sediments ranges from 0 to 3.4 percent by weight. In general, high values are associated with fine-grained sediments and deep water; low values are associated with coarse-grained sediments and relatively shallow water. There is an apparent trend for deep water sediments near shore to contain more organic matter than samples taken at similar depths farther from shore.

The quantitative geographic distribution of sediment organic matter is illustrated in figure 9. Sediments with highest organic content occurred in the deep-water (greater than 100 fathoms) basin northwest of Georges Bank. Sediments in this area are composed predominantly of silts and clays, with a median particle size less than 0.05 mm. The organic content in these samples ranges from 3.0 to 3.4 percent. In somewhat shallower water adjacent to this basin the sediment organic content is, on the average, between 0.5 and 3.0 percent. The lower values usually occur at the shallower depths.

North of Great South Channel and Georges Bank in water depths greater than 100 fathoms, there is a striking offshore (west to east) gradient in organic content. Sediment samples taken farthest offshore are markedly lower in organic content than samples taken nearer the Massachusetts coast. Organic matter in near shore samples ranges from 2.2 to 3.4 percent, compared to 0.1 percent or less in the easternmost samples.

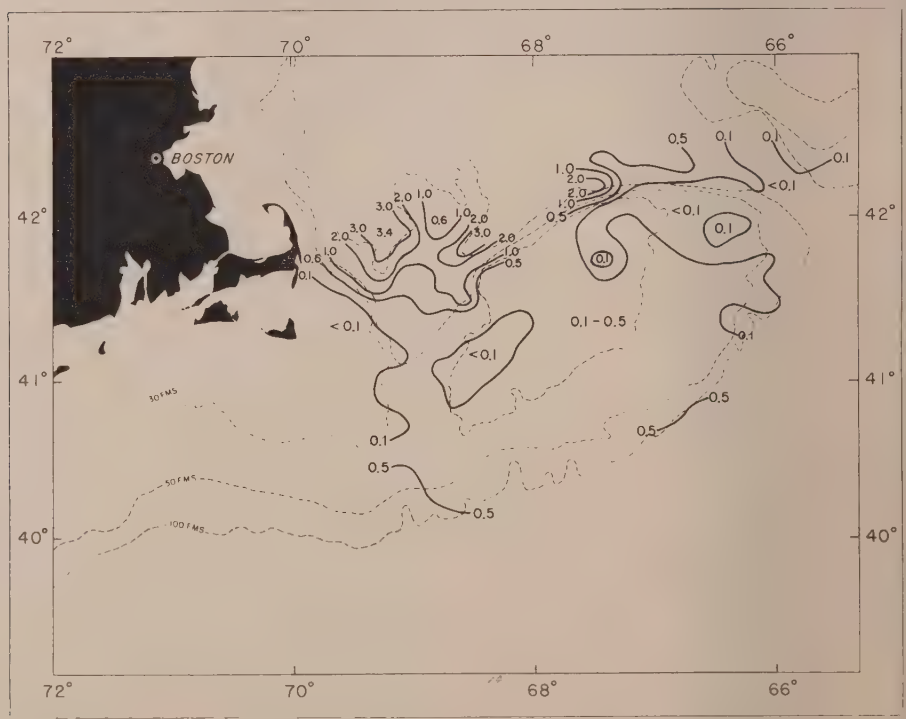

FIG. 9.—Quantitative geographic distribution of sediment organic matter. Values are given in percentage weight.

Relationship with Water Depth—The relationship between water depth and sediment organic content is difficult to assess from the isopleth chart shown in figure 9, because of geographic variations. A summation of the same data upon which the chart is based is listed in table 3. The mean organic content for each 25-fathom depth class is listed separately for both the eastern and western halves of the study area (see inset in figure 6 for division between the eastern and western sections). This tabulation shows clearly the relationship of organic matter and water depth, and also the difference in degree of correlation in this relationship between the eastern and western sections.

On Georges Bank proper, nearly all sediments contain less than 1.0 percent organic matter. Moreover, it is 0.2 percent or less in more than 85 percent of all sediment samples taken within the bank's 50-fathom isobath. Organic content of 0.1 and 0.2 percent are by far the most common values for Georges Bank sediments. Two areas where sediments are especially low, less than 0.1 percent, in organic matter are: (1) the bank's northeastern end, and (2) a small sector in the shallow part of southwestern Georges Bank.

In Eastern Channel and southwestern Browns Bank the sediment organic content is also very low—0.1 percent or less. Sediments from the shallow portion of Great South Channel are likewise low in organic matter, ranging from 0.2 to less than 0.1 percent. However, in the southern part of this channel, in water depths between 40 and 100 fathoms, the organic content is slightly higher, containing 0.4 to 0.7 percent.

In the western half of the study area there is a pronounced increase in organic content with increased depth of water. This same trend exists in the eastern half, but the increment is exceedingly small. In the western section the organic matter ranges in quantity from 0.1 percent in the 0–24 fathom depth class to 2.5 percent in the 100–124 fathom depth class. In the eastern section it gradually increases from 0.1 percent in the 0–24 fathom depth class to only 0.4 percent in the 175–199 fathom depth class.

Two principal factors that affect the quantity of organic matter in bottom sediments are (1) water currents and (2) oxygen content of the overlying water (Trask, 1939; Richards and Redfield, 1954). In the Georges Bank area, water currents appear to be the primary determinant. Rather strong currents prevail over the shallow portions of the bank and also over the bank's eastern end and adjacent deep water (Bigelow, 1927). In these same areas the sediment organic content is low. The areas where the organic content is high—the deep water section northwest of Georges Bank—are areas where bottom water currents are weak.

TABLE 3.—*Mean sediment organic content in eastern and western sections of the study area*

Water depth class (fathoms)	Mean organic content (percentage weight)	
	Eastern	Western
0–24	0.1	0.1
25–49	0.1	0.2
50–74	0.1	0.4
75–99	0.2	1.0
100–124	0.1	2.5
125–149	0.4	—
150–174	0.4	—
175–199	0.4	—

Oxygen content of the water just above the sediments also appears to play an important role in affecting the variations in amount of sediment organic matter from place to place in the Georges Bank region. Oxygen content of bottom water (Rakestraw, 1933) on Georges Bank is significantly higher than bottom water in the southern Gulf of Maine. Also, there is more rapid replenishment of oxygen in bottom water on Georges Bank than in the adjacent deep-water north of the bank. Thus the decomposition of organic matter on Georges Bank would be accelerated by the higher oxygen concentration. It is concluded that oxygen and water currents are two of the principal factors producing the wide geographic variations in sediment organic content observed in this area.

Relationship with Sediment Particle Size—The physical factors involved in the deposition and erosion of sediments likewise affect the deposition of organic matter. This results in a close correlation between organic content and sediment particle size. In the Georges Bank area, as in most others, organic content is high in fine-grained sediments and low in coarse-grained sediments.

TABLE 4.—*Relationship between sediment particle size and quantity of organic matter*

Median particle size (mm)	Organic matter (percent)	Number of samples
0.01	3.27	3
0.02	2.40	5
0.07	1.70	5
0.16	0.83	15
0.25	0.50	30
0.35	0.29	24
0.44	0.22	14
0.69	0.22	63
1.31	0.09	25
2.14	0.08	4
3.36	0.08	2
4.93	0.13	6
8.92	0.06	6
12.34	0.10	6
15.00	0.10	1
18.50	0.06	6
22.75	0.06	8

This is evident from table 4, where percentage organic content is listed opposite median particle size. This relationship is significant only in those sediments having a median diameter less than about 2 mm. In sediments with a median diameter 2 mm or more, there is little change in organic content associated with an increase in diameter. A decrease in median diameter from 2.0 to 0.5 mm is accompanied by a slight increase in organic matter, from 0.08 to 0.20 percent. In contrast to this, a sharp increase in organic content, from 0.2 to 3.3 percent, is associated with a decrease in median diameter from 0.5 to 0.01 mm.

Additional evidence on this subject is shown in figure 7, in which profiles of sediment median diameter and organic content are plotted for two transects across Great South Channel. Although variations occur, the general trend described above is evident.

Shell Content

Mollusk shell fragments constitute a significant portion of the sediments in some localities and, due to their peculiar physical characteristics, they are of special importance from the biological standpoint. For example, certain species of tube-building polychaete worms select only mollusk shell fragments from the sediment for tube construction. The measure of shell content derived from this study are minimum values only, inasmuch as they are based on fragments 2 mm in diameter or larger. Obviously smaller particles of shell are present in the sediments, but the additional labor required to obtain more refined values was not warranted. Shell content values are expressed as percentage weight of the total sediment sample. Values for each sample are listed in column 9 of table 2, and illustrated in figure 10.

Shell fractions in the sediment samples range from 0 to 25 percent. Shell is most prevalent in sediments from the eastern part of Georges Bank. A rather broad band across the bank's eastern end, extending from the northern edge southward and westward to the southern edge, encompasses an area where most of the sediments consist of 5 to 25 percent shell. Relatively high percentages of shell also occur at a few localized areas in Great South Channel. Sediments in the central and western parts of Georges Bank are composed of rather small quantities of shell, generally less than 2 percent. In water depths greater than 75 fathoms along the entire northern edge, shell fragments are very sparse or absent. The geographic distribution of shell fragments agrees rather closely with the occurrence of sea scallop (*Placopecten magellanicus*) beds. The sea scallop is the only shellfish currently being fished commercially on this bank.

The relationship between water depth and shell content is shown in figure 11. It is apparent from this graph that shell fragments are most abundant in sediments occurring between 15 and 75 fathoms in depth. In depths greater than 75 fathoms the quantity of shell is consistently very low, less than 0.1 percent in most cases.

Color

Variations in sediment color from white to dark gray brown are found distributed in a somewhat random pattern over the entire area studied (see column 10 in table 2). Browns, grays, and combinations of the two colors are especially common. There is a trend for the light colored sediments, such as white and yellow, to be more common in the central and south central parts of Georges Bank. Darker sediments are predominant in

FIG. 10.—Quantitative geographic distribution of mollusk shell fragments. Values are given in percentage weight.

the channels and deep-water areas. Sediments with high organic content are generally gray in color, but this relationship is not consistent. There is no distinct association between color and particle size or other sediment parameters.

DISCUSSION

Georges Bank sediments consist mainly of sand of various sizes. This material is mostly glacial debris. At the present time very little new sediment is being deposited on the bank proper. Silts and clays of terrigenous origin, which may be expected to be discharged from rivers in northern New England and southeastern Canada and carried to the bank in suspension, appear to be effectively trapped in the Gulf of Maine basin before reaching the bank. Changes in sediment distribution now taking place result primarily from the shifting and remolding of material already present on the bank.

The generalization that sediments are finer in the deep water farther from land

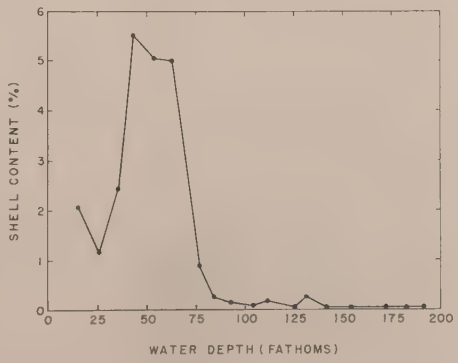

FIG. 11.—Relationship between water depth and sediment shell content.

than those occurring in shallower water close to shore, does not apply to the Georges Bank area. Some strikingly different relationships between sediment particle-size and water depth and distance from land are illustrated in figure 12. Two transects of sediment samples extending from shallow to deep water, one near-shore and one offshore, reveal nearly opposite trends in size distribution versus water depth. In this figure the particle-size frequency distributions are illustrated in their respective positions below the water depth profile. These examples are based on sediments taken at stations 1–9 for the near-shore transect, and from stations 162–153 for the offshore transect (see inset in figure 12 for locations).

From figure 12 it can be seen that in near-

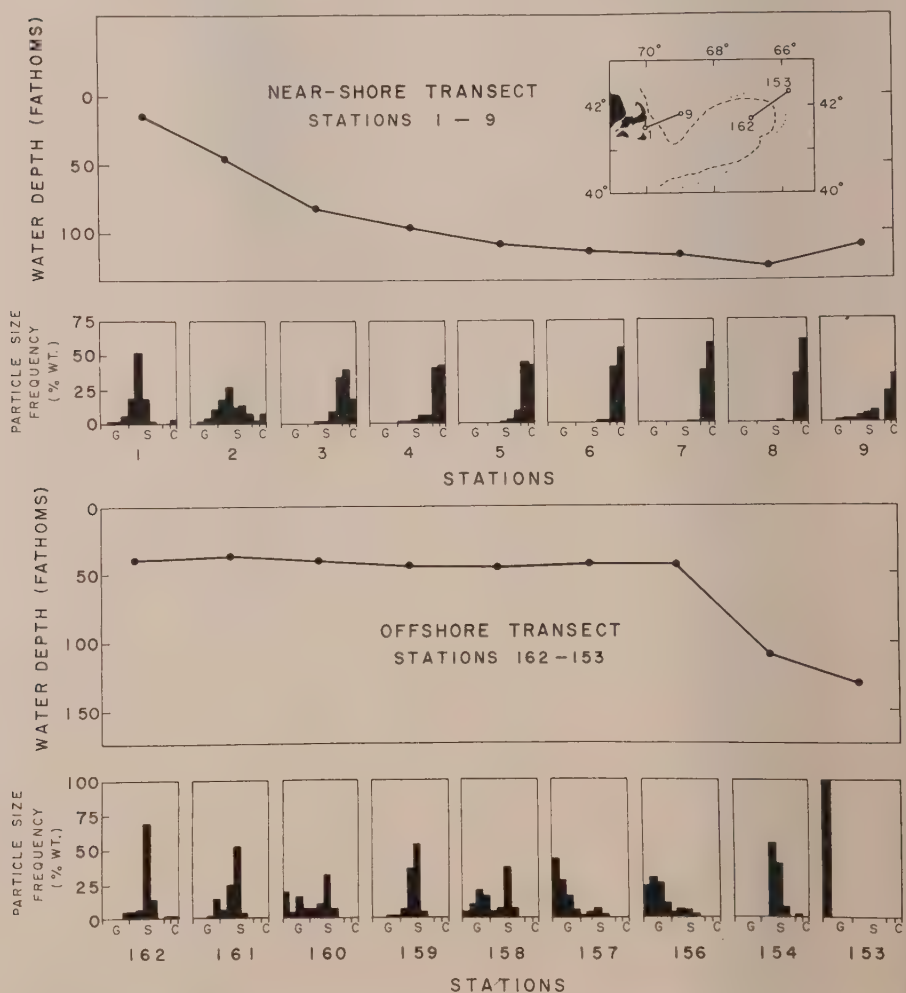

FIG. 12.—Sediment particle size in relation to water depth for samples from two transects, (1) near-shore and (2) offshore, extending from shallow to deep water. Abbreviations of sediment fractions are: gravel—G, sand—S, and clay—C.

shore sediments, gravel and sand predominate in samples from shallow water, and silt and clay successively increase in deeper water samples. At stations 6, 7, and 8 the sediments are very similar to one another, each consisting predominantly of clay with silt ranking second. Another feature revealed by this figure is the increase in sand and gravel at station 9, where the water depth is slightly less than at preceding stations.

Sediments taken along the offshore transect exhibit a trend distinctly opposite to the foregoing. Shallow water sediments are generally finer than those from the deep water. At the shallow water stations (162-156), in depths of approximately 40 fathoms, the sediment is composed largely of sand and gravel, plus small quantities of silt and clay. At the deepest station (153), in 129 fathoms, the substrate is entirely gravel.

Our knowledge of the hydrography of the Georges Bank area, especially in regard to current velocity of bottom water, is still too imperfect to adequately understand the relationships between water movement and sedimentation. It is known that wave action extends to the bottom over most of Georges Bank in winter, and that tidal currents are exceptionally strong on the bank's shallower portions throughout the year. The effectiveness of the combination of wave action and tidal currents in sorting bottom deposits in the shallower parts of the bank is indicated by the large expanse of central and southern Georges Bank where sediments are very well sorted. In some deep-water areas, especially in and near the channels at the eastern and western ends of the bank, the non-tidal current is probably the main sorting agent.

Further evidence of complex sedimentary processes associated with hydrographic conditions is evident from the geographic distribution of organic matter. Sediment organic content is low not only in the shallow portions of Georges Bank, where wave action and tidal currents are operative, but also in some deep-water areas adjacent to the bank.

SUMMARY

1.—Sand is by far the most prevalent sediment on Georges Bank and vicinity. Gravels are common in the channels and on the northern and eastern parts of the bank. Silts and clays are predominant only in the deep-water basin northwest of Georges Bank.

2.—Sediment median diameters ranged from 0.01 to 22.75 mm. A large portion of the study area contains sediments whose median diameters are between 0.25 and 1.0 mm. Greatest variation in median diameters occurs in the channel areas and along the bank's northern periphery.

3.—Natural sorting of the sediment fractions ranges from poorly sorted to perfectly sorted. Poorly sorted sediments predominate in the channels and on the northern edge of Georges Bank. Well sorted sediments occur over a large area in the central and southern sections of Georges Bank, and small patches are found in the channel areas and along the bank's northern edge.

4.—Organic content varies directly with the sediment silt-clay content. The organic content ranges from 0 to 3.4 percent, and is highest in the silt-clay sediments northwest of Georges Bank. Generally, very small quantities (less than 0.5 percent) of organic matter are present in the sediments on Georges Bank proper.

5.—Mollusk shell fragments comprise a significant portion of the sediments in some localities. They are especially common in a north-south band extending across the eastern end of Georges Bank. Sediments with as much as 25 percent shell are found in this area. Over most of the bank the sediments contain less than 2 percent shell, and in deep water the shell content is nil.

6.—A rather wide variety of sediment colors was observed. They range from white to dark gray brown. Brown and gray and combinations of these two colors are most common.

ACKNOWLEDGMENTS

I wish to thank Dr. Robert L. McMaster, Narragansett Marine Laboratory, and Dr. H. T. Greweling, N. Y. State College of Agriculture, for helpful suggestions and advice.

APPENDIX

TABLE A.—*Coordinates of latitude and longitude for each station, and the sediment particle-size distribution mean, kurtosis and two measures of skewness*

Station Number	Station Latitude (North)	Location Longitude (West)	Sediment sample parameters				
			Mean diameter ($M\phi$)	Median diameter ($Md\phi$)	Skewness ($\alpha_{1\phi}$)	Skewness ($\alpha_{2\phi}$)	Kurtosis (β_ϕ)
1	41°36′	69°47′	−0.15	−0.10	−0.06	−0.39	1.08
2	41°40′	69°42′	0.55	0.20	0.17	1.41	1.63
3	41°42′	69°38′	4.45	3.90	0.31	0.69	0.60
4	41°46′	69°33′	5.45	5.80	−0.18	−0.44	0.67
5	41°48′	69°28′	5.70	5.80	−0.06	−0.11	0.56
6	41°51′	69°22′	6.15	6.20	−0.04	−0.26	0.82
7	41°55′	69°15′	6.30	6.20	0.11	−0.06	0.28
8	41°57′	69°10′	6.35	6.40	−0.04	−0.13	0.60
9	42°00′	69°05′	3.20	4.60	−0.45	−0.68	0.61
10	41°54′	69°05′	5.95	6.10	−0.09	−0.14	0.23
11	41°49′	69°05′	5.80	5.70	0.56	0.03	0.25
12	41°45′	69°04′	3.95	4.00	−0.02	−0.46	0.73
13	41°39′	69°06′	1.85	1.60	0.12	0.56	1.09
14	41°34′	69°06′	0.65	1.20	−0.17	−0.14	1.02
15	41°30′	69°05′	0.90	1.00	−0.13	−0.44	0.81
16	41°25′	69°06′	−0.55	−0.20	−0.14	0.06	0.67
17	41°19′	69°05′	−1.55	−2.10	0.20	0.47	0.40
18	41°14′	69°05′	0.15	0.60	−0.21	0.33	1.37
19	41°09′	69°04′	−0.75	−0.30	−0.23	−0.31	0.38
20	41°05′	69°05′	0.35	0.50	−0.43	−0.86	1.00
21	40°59′	69°06′	−0.80	0.90	−0.81	−0.90	0.33
22	40°54′	69°05′	−1.65	−1.20	−0.16	−0.14	0.16
23	40°48′	69°04′	−1.85	−2.50	0.22	0.27	0.11
24	40°43′	69°04′	−0.80	−0.10	−0.41	−0.59	0.47
25	40°38′	69°04′	−0.60	0.70	−0.68	−0.76	0.50
26	40°33′	69°06′	1.50	1.50	0.00	−0.20	1.00
27	40°29′	69°06′	2.55	2.40	1.00	7.00	6.00
28	40°24′	69°06′	2.70	2.50	0.50	2.63	2.88
29	40°19′	69°05′	2.70	2.70	0.00	2.40	2.40
30	40°14′	69°05′	2.25	2.80	−1.00	0.27	3.45
31	40°10′	69°05′	2.00	2.20	−0.13	0.06	1.00
32	40°09′	68°58′	2.30	2.60	−0.25	−0.88	1.54
33	40°09′	68°50′	2.15	2.10	0.77	1.15	1.85
34	40°15′	68°50′	1.75	1.80	−0.05	0.43	0.76
35	40°20′	68°51′	1.80	1.90	−0.11	−0.06	0.61
36	40°26′	68°51′	2.30	2.30	0.00	0.66	1.33
37	40°29′	68°52′	−4.50	−4.50	0.00	0.00	−1.00
38	40°34′	68°51′	3.55	2.20	0.69	0.74	0.15
39	40°39′	68°51′	−0.20	0.60	−0.42	−0.58	0.32
40	40°44′	68°51′	−1.00	0.50	−0.79	−1.08	0.50
41	40°52′	68°50′	−1.15	0.90	−0.80	0.90	0.25
42	40°55′	68°50′	−0.55	0.60	−0.11	−0.56	1.56
43	41°00′	68°50′	0.10	0.50	−0.36	−0.68	0.59
44	41°05′	68°50′	−3.45	−3.50	0.05	1.67	1.62
45	41°10′	68°50′	0.60	1.30	−0.54	−1.11	0.88
46	41°15′	68°50′	0.10	1.20	−0.69	−1.31	0.88
47	41°20′	68°50′	1.25	1.80	−0.48	−1.26	1.13
48	41°25′	68°50′	2.30	2.20	0.20	0.60	1.00
49	41°30′	68°50′	1.75	2.60	−0.59	0.10	1.17
50	41°34′	68°50′	2.90	3.20	−0.21	−0.39	1.96
51	41°39′	68°50′	1.70	2.40	−0.26	−0.04	0.66
52	41°44′	68°50′	3.35	3.60	−0.08	−0.33	0.66
53	41°50′	68°50′	2.45	2.00	0.12	0.15	0.30
54	41°54′	68°50′	0.85	0.60	0.19	1.44	1.93
55	42°00′	68°50′	1.40	1.30	0.06	0.63	1.44
56	41°55′	68°46′	0.80	0.60	0.07	0.50	0.69

TABLE A.—*Continued*

Station Number	Station Latitude (North)	Location Longitude (West)	Sediment sample parameters				
			Mean diameter (Mϕ)	Median diameter (Mdϕ)	Skewness ($\alpha_{1\phi}$)	Skewness ($\alpha_{2\phi}$)	Kurtosis (β_ϕ)
57	41°52′	68°42′	2.75	2.00	0.26	0.28	0.51
58	41°47′	68°38′	3.05	3.10	−0.08	−0.08	1.08
59	41°42′	68°35′	4.15	3.60	0.44	1.12	0.92
60	41°39′	68°30′	2.00	1.40	0.27	0.70	0.93
61	41°35′	68°26′	−0.15	0.30	−0.24	−0.27	0.35
62	41°31′	68°23′	−0.25	1.10	−0.60	−0.93	0.44
63	41°26′	69°19′	1.70	1.50	1.00	2.25	1.25
64	41°22′	68°20′	−0.05	0.00	−0.11	−0.22	1.00
65	41°18′	68°11′	−0.35	−0.40	0.20	0.40	1.80
66	41°14′	68°07′	0.75	0.90	−0.27	−1.18	1.45
67	41°10′	68°03′	0.50	0.60	−0.25	−0.25	0.75
68	41°06′	68°00′	1.10	1.50	−4.00	5.00	4.00
69	41°02′	67°56′	1.70	1.90	−0.67	−0.50	1.17
70	40°57′	67°52′	2.00	2.00	0.00	−0.33	1.00
71	40°53′	67°48′	0.95	0.80	0.18	0.24	0.76
72	40°49′	67°49′	0.80	1.00	−0.36	−0.55	1.18
73	40°45′	67°40′	1.05	1.00	0.07	0.13	0.87
74	40°41′	67°36′	1.85	2.10	−0.29	−0.41	1.06
75	40°36′	67°33′	0.95	1.00	−0.09	−0.27	1.09
76	40°32′	67°33′	0.55	1.00	−0.47	−0.37	0.95
78	40°33′	67°28′	1.40	1.40	0.00	0.06	0.69
79	40°37′	67°28′	0.25	0.30	−0.08	−0.31	1.15
80	40°43′	67°29′	1.45	1.40	0.06	0.18	0.59
81	40°48′	67°23′	1.50	1.40	0.13	0.00	0.75
82	40°53′	67°28′	1.65	1.70	−0.08	0.00	1.31
83	40°59′	67°28′	1.25	1.50	−0.45	0.36	1.18
84	41°04′	67°28′	1.35	1.40	−0.09	0.00	0.64
85	41°09′	67°28′	1.80	1.90	−0.25	−0.50	0.75
86	41°14′	67°28′	1.55	1.50	0.14	0.14	0.86
87	41°19′	67°28′	0.40	0.50	−0.13	−0.25	0.50
88	41°24′	67°28′	0.80	1.10	−0.60	−1.40	1.20
89	41°29′	67°28′	1.05	1.00	0.11	0.33	0.67
90	41°34′	67°28′	−0.10	0.30	−0.50	−0.75	0.75
91	41°39′	67°28′	−1.80	−4.20	0.89	0.94	0.06
92	41°44′	67°28′	−0.60	−0.50	−0.05	−0.13	0.48
93	41°49′	67°28′	−2.15	−3.70	0.66	0.89	0.23
94	41°54′	67°28′	−1.20	−2.40	0.50	0.48	0.19
95	42°01′	67°27′	−2.00	−3.40	0.56	0.70	0.14
96	42°05′	67°28′	−0.20	0.60	−0.42	−0.37	0.26
97	42°08′	67°28′	2.55	2.30	0.33	0.87	0.80
98	42°10′	67°28′	4.55	3.90	0.39	0.76	0.55
99	42°16′	67°27′	2.65	1.90	0.33	0.62	0.69
100	42°20′	67°28′	−1.30	−3.70	0.75	0.97	0.59
101	42°20′	67°20′	0.75	1.70	−0.33	−0.47	0.53
102	42°20′	67°10′	2.15	2.50	−0.14	−0.39	1.06
103	42°15′	67°10′	2.00	2.00	0.00	1.00	1.00
104	42°10′	67°10′	−1.85	−3.90	0.77	1.02	0.25
105	42°07′	67°09′	−0.60	−0.40	−0.18	−0.27	0.36
106	42°06′	67°09′	−1.20	−1.00	−0.12	−0.12	0.29
107	42°00′	67°10′	2.55	2.50	1.00	10.00	9.00
108	42°00′	67°04′	1.10	1.10	0.00	0.00	1.00
109	42°02′	66°58′	0.60	0.60	0.00	0.50	1.00
110	42°00′	66°56′	0.15	0.20	−0.11	−1.11	1.67
111	42°00′	66°45′	−1.00	−0.80	−0.10	0.05	0.30
112	42°05′	66°45′	−2.20	−3.70	0.65	0.91	0.26
113	42°07′	66°45′	−4.50	−4.50	0.00	0.00	0.00
114	41°10′	66°45′	−0.25	0.40	−0.62	−0.86	0.71

(*Table continues on next pages*)

TABLE A.—*Continued*

Station Number	Station Latitude (North)	Location Longitude (West)	Sediment sample parameters				
			Mean diameter ($M\phi$)	Median diameter ($Md\phi$)	Skewness ($\alpha_{1\phi}$)	Skewness ($\alpha_{2\phi}$)	Kurtosis (β_ϕ)
115	42°15′	66°45′	2.00	2.40	−0.31	−0.19	1.96
116	42°20′	66°45′	1.00	1.60	−0.25	0.06	0.77
117	42°20′	66°40′	1.45	1.80	−0.21	0.06	1.48
118	42°21′	66°31′	−1.45	−0.80	−0.21	−0.07	0.15
119	42°21′	66°26′	−1.65	−2.10	0.16	0.30	0.14
120	42°21′	66°21′	−3.35	−4.50	1.00	2.30	1.48
121	42°15′	66°21′	−0.60	0.50	−0.48	−0.65	0.52
122	42°10′	66°20′	0.00	0.70	0.00	−0.27	0.32
123	42°07′	66°20′	−1.80	−0.30	−0.56	−0.41	0.15
124	42°04′	66°20′	−2.30	−3.00	0.33	0.57	0.29
125	42°00′	66°20′	−2.95	−4.50	1.03	1.84	0.84
126	41°55′	66°20′	−2.30	−3.20	0.45	0.75	0.40
127	41°50′	66°20′	−0.55	0.10	−0.57	−0.70	0.39
128	41°45′	66°20′	0.60	0.70	−0.25	−0.50	1.00
129	41°41′	66°20′	0.45	0.60	−0.20	−0.87	1.33
130	41°35′	66°19′	0.35	0.50	−0.23	−0.54	0.92
131	41°29′	66°21′	−0.30	0.20	−0.29	−0.38	0.56
132	41°24′	66°20′	−0.05	0.50	−0.33	−0.33	0.30
133	41°24′	66°14′	1.20	1.70	−0.56	−0.72	0.39
134	41°24′	66°07′	−1.65	−1.60	−0.02	0.07	0.09
135	41°24′	66°00′	−1.05	−1.30	0.12	0.17	0.24
136	41°30′	66°00′	−0.25	0.10	0.20	−0.34	0.49
137	41°35′	66°00′	0.50	0.60	−0.17	0.08	0.58
138	41°40′	66°00′	−0.50	0.20	−0.50	0.54	0.39
139	41°45′	66°00′	0.60	0.60	0.00	−0.25	1.00
140	41°49′	65°58′	−0.65	−0.70	0.03	0.12	0.21
141	41°52′	65°54′	−2.00	−2.20	0.08	0.20	0.12
142	41°55′	65°48′	−3.50	−4.50	1.00	2.85	1.85
144	42°03′	65°39′	−4.10	−4.50	1.00	1.75	0.75
146	42°09′	65°30′	−4.10	−3.00	0.38	0.48	0.18
148	42°17′	65°38′	−2.10	−4.20	0.88	1.08	0.21
149	42°20′	65°44′	−2.10	0.50	0.38	0.48	0.18
150	42°22′	65°47′	−1.50	0.20	−0.67	0.78	0.05
151	42°18′	65°51′	−1.45	−0.80	−0.45	0.59	0.76
152	42°15′	65°56′	−1.95	−1.90	−0.03	0.05	0.23
153	42°11′	66°02′	−4.50	−4.50	—	—	—
154	42°09′	66°06′	0.80	0.50	1.00	0.20	1.00
156	42°02′	66°16′	−3.05	−3.50	0.31	1.07	0.76
157	41°57′	66°21′	−3.45	−4.20	0.71	2.43	1.71
158	41°58′	66°25′	−1.10	−1.00	−0.04	−0.17	0.26
159	41°50′	66°30′	0.45	0.60	−0.23	−0.46	0.69
160	41°46′	66°34′	−1.60	−0.60	−0.34	−0.29	0.05
161	41°42′	66°41′	−0.15	0.60	−0.65	−0.91	0.52
162	41°40′	66°45′	1.00	1.40	0.80	2.60	2.20
163	41°35′	66°45′	1.00	1.30	−0.60	2.30	2.30
164	41°29′	66°45′	1.15	1.20	−0.14	0.00	1.00
165	41°25′	66°44′	−1.45	−0.30	−0.38	0.30	0.08
166	41°19′	66°45′	0.45	0.50	−0.09	−0.27	0.91
167	41°14′	66°44′	0.95	0.90	0.11	−0.11	0.89
168	41°09′	66°45′	0.40	0.40	0.00	−0.17	0.67
169	41°05′	66°44′	0.60	0.70	−0.20	−0.60	1.20
170	40°59′	66°44′	1.45	1.40	0.14	0.14	0.86
171	40°54′	66°46′	1.40	1.50	−0.25	−0.50	1.00
172	40°49′	66°45′	2.40	2.30	0.17	0.67	0.83
173	40°49′	66°52′	0.75	0.80	−0.09	−0.09	0.73
174	40°48′	66°58′	1.85	1.90	−0.11	−0.67	0.78
175	40°48′	67°05′	1.65	1.70	−0.09	−0.36	0.82
176	47°47′	67°12′	2.10	2.00	0.20	1.00	1.00

TABLE A.—*Continued*

Station Number	Station Latitude (North)	Location Longitude (West)	Sediment sample parameters				
			Mean diameter ($M\phi$)	Median diameter ($Md\phi$)	Skewness ($\alpha_{1\phi}$)	Skewness ($\alpha_{2\phi}$)	Kurtosis (β_ϕ)
177	40°46′	67°18′	2.10	2.20	−0.14	−0.28	0.71
178	40°46′	67°25′	1.60	1.50	0.13	0.19	0.81
179	40°46′	67°32′	1.45	1.50	−0.06	0.18	0.59
180	40°46′	67°37′	0.60	0.60	0.00	0.64	0.50
181	40°46′	67°45′	−0.30	0.10	−0.33	−0.29	0.54
182	40°46′	67°52′	1.25	1.30	−0.11	0.00	0.78
183	40°48′	67°58′	1.75	1.80	−0.11	−0.44	1.00
184	40°48′	68°06′	1.65	1.80	−0.27	−0.55	0.64
185	40°48′	68°12′	1.95	1.90	0.20	0.80	1.40
186	40°48′	68°19′	1.70	1.60	0.33	1.00	1.00
187	40°48′	68°25′	0.20	0.30	−0.25	−0.38	0.63
188	40°48′	68°32′	0.90	1.00	−0.20	−0.30	0.90
189	40°48′	68°40′	−0.55	−0.20	−0.23	−0.13	0.55
190	40°48′	68°46′	0.70	0.50	0.22	0.33	0.56
191	40°48′	68°59′	−0.60	0.70	−0.54	−0.67	0.38
192	40°48′	69°02′	1.00	1.10	−0.17	−2.50	3.00
193	40°48′	69°06′	−0.30	0.00	−0.38	−0.56	0.69
194	40°48′	69°13′	1.20	0.00	−0.57	−0.62	0.24
195	40°48′	69°15′	−2.05	−4.20	0.88	1.04	0.16
196	40°52′	69°15′	−1.15	0.70	−0.76	−0.88	0.20
197	40°58′	69°15′	−1.25	−0.40	−0.33	−0.33	0.27
198	41°00′	69°15′	−0.60	−0.40	−0.48	−0.57	0.38
199	41°00′	69°08′	−2.50	−3.60	0.38	0.41	0.31
200	41°00′	69°02′	−1.10	0.30	−0.64	−0.61	0.30
201	41°00′	68°55′	−1.00	−0.40	−0.24	−0.26	0.26
202	41°00′	68°48′	0.35	0.30	0.07	3.87	4.73
203	41°00′	68°42′	−2.05	−2.50	0.20	0.47	0.36
204	41°00′	68°35′	−0.75	−0.40	−0.19	−0.30	0.32
205	41°05′	68°35′	−1.05	0.00	−0.45	−0.53	0.26
206	41°10′	68°35′	−1.20	−0.60	−0.32	−0.32	0.21
207	41°15′	68°35′	−0.50	1.20	−0.77	−0.80	0.34
208	41°20′	68°35′	2.80	2.30	0.83	3.83	4.67
209	41°25′	68°35′	2.35	2.50	−0.27	3.00	5.64
210	41°30′	68°35′	1.00	0.60	0.24	0.26	0.26
211	41°34′	68°34′	0.65	0.80	−0.05	0.51	1.09
213	41°45′	68°34′	1.70	2.10	0.18	0.32	1.36
214	41°45′	68°28′	1.15	0.80	0.13	0.15	1.15
215	41°45′	68°22′	3.65	3.10	0.23	0.60	0.79
216	41°40′	68°24′	0.50	0.40	0.17	0.92	1.25
217	41°34′	68°25′	−0.75	−0.50	−0.09	−0.15	0.25
218	41°30′	68°28′	1.95	1.80	0.33	1.22	0.89
219	41°24′	68°31′	1.90	2.20	−0.50	−2.58	3.42
220	41°25′	68°37′	2.20	2.40	−0.40	−1.00	1.80
221	41°25′	68°44′	2.10	1.80	0.43	0.57	0.86
222	41°25′	68°50′	0.50	1.50	−0.46	−0.48	0.39
223	41°25′	68°57′	1.20	1.50	−0.18	0.38	1.62
224	41°25′	69°05′	0.45	1.20	−0.41	0.30	1.30
225	41°25′	69°12′	−0.50	0.30	−0.33	−0.29	0.40
226	41°25′	69°18′	0.85	1.20	−0.23	−0.58	0.81
227	41°25′	69°25′	−2.50	−3.10	0.30	0.58	0.28
228	41°25′	69°30′	−4.50	−4.50	0.00	0.00	−1.00
229	41°25′	69°34′	−2.10	−3.20	0.46	0.61	−0.06

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NATURAL HISTORY OF A SELECTED SPECIES OF MARINE INVERTEBRATE

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Background:

Compared with other animal groups such as birds, mammals, and fishes, relatively little is known about the natural history of marine invertebrates. A few species of commercial importance, namely the oyster, American lobster, blue crab, several species of clams and the larger southern shrimps, have been rather carefully studied. However, there are numerous species that are abundant and have a wide geographic distribution about which our information is exceedingly meager. Some of these unstudied animals serve as vital links in the food cycle by providing nourishment for commercial fishes. Moreover, the time is fast approaching when some of these organisms will be harvested for human consumption. New and important contributions to our knowledge of these animals can be obtained from independent studies at various localities along our coasts.

Suggested Approach:

First, make a few exploratory collecting trips to several different bays, marshes, or other likely places--preferably near your home. Select collecting sites where there is a reasonably large area of shallow water, generally less than 3 or 4 feet in depth. Collect some marine invertebrates (shrimp, crabs, mollusks, annelid worms, and similar forms). Try to sample different types of habitats.

After examining these collections select one area and one species that is plentiful and interests you. Identify the species and have the identification verified by a scientist at a nearby university or biological station. It is very important that the exact species be determined. Also, learn to distinguish closely related species to avoid inadvertently including other species in your samples.

Proceed to collect a sample of about 50 specimens every month or two. Preserve these specimens in a solution of 10 percent formalin. A major segment of this study consists of making careful observations and faithfully recording them. Instructions and examples of the kinds of measurements to make and records to keep are given in Lagler (1952) (Chapter I.)

A few life history aspects you should consider for study are: (a) seasonal occurrence, (b) abundance or density, (c) food and feeding habits, (d) size and age composition, (e) sex ratio, (f) growth rate, (g) spawning habits (see Lagler op. cit.). Some of these will be correlated with physical factors such as water temperature, stage of the tide, light intensity, and weather conditions. Details of how to study these various aspects and to correlate them with specific physical factors are described in the references. Plan some night collecting trips and take advantage of unusual hydrographic conditions to study their influence on the species. It would be much to your advantage to correspond with a scientist who has had practical experience in conducting studies of this kind.

Possible Pitfalls:

In your study, give priority to those natural history aspects the study of which you can adequately complete. Beware of being stalled on those aspects which are obviously beyond your facilities and capabilities. For example, if the stomach contents are composed of very small organisms that are difficult to identify or are finely fragmented, forego the food habits study in favor of other research until your experience warrants further pursuit.

For every hour spent in the field observing and collecting specimens, plan to spend several hours in the laboratory carefully studying and processing this material.

Observe local laws and state regulations concerning seining, collecting, shellfishing and so forth.

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BENTHIC FAUNA OF GEORGES BANK

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BENTHIC FAUNA OF GEORGES BANK

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For over 300 years fishing has been a major industry in the coastal New England States. The bountiful supply of fishes available to the the Pilgrims and their contemporaries was a prime factor enabling them to successfully colonize this region. Later, the fishing industry played a fundamental role in colonial New England's commerce and was a key to its prosperity (Ackerman 1941). The backbone of this fishing industry at the present time is the bottom-dwelling group of fishes, called groundfish, which includes such species as cod, haddock, several hakes, and flounders. These fish spend most of their lives in the vicinity of the sea floor, feeding on invertebrate animals and the smaller fishes that abound in that stratum. The so-called benthic and epi-benthic organisms are the principal source of nourishment for these vast stocks of commercially valuable fishes.

The importance of an adequate food supply for fish has been recognized for centuries. This has resulted in numerous investigations of the food, feeding, and availability of foods for many species of fish (Dean 1923, FAO 1958-60). As the habitat for many stocks of fishes is continually being diminished and many stocks fished commercially and by sportsmen are dwindling in number, it is only by chance or guesswork that wise use can be made of our fishery resources unless the ecological aspects are clearly understood.

Our knowledge of New England marine life was greatly enhanced by such illustrious zoologists as Professors Louis Agassiz, Addison Verrill, and Sidney Smith. These and a number of other nineteenth century zoologists faced a vast unstudied fauna. The staggering taxonomic problems consumed a large share of their time. And, of course, proper classification is a necessary prerequisite for most ecological studies. However, in this particular region, the general sequence of interest took a peculiar turn. Interest switched from taxonomic inquiry to physiological studies, with relatively little effort devoted to ecological aspects. This turn of events is particularly true in respect to the benthic fauna studies.

In recent years the necessity for information about all aspects of marine life, including the benthos, has been rising rapidly. Not only is there academic interest in this sphere, but the need arising from increased demands for more efficient fisheries management, the possibility of using the oceanic environment for warfare, and the disposal of atomic wastes in our offshore waters have created a vital need to

understand the life and waters of our seas. Not the least of these is the biological realm on the New England Continental Shelf.

GEORGES BANK

Georges Bank is a relatively shallow sill extending between Massachusetts and Nova Scotia at the mouth of the Gulf of Maine. Since this bank is roughly 12,000 square miles in area, it forms a significant portion of the New England Continental Shelf. As such, it is the largest fishing bank in this region, and is one of the most productive fishing grounds in the world. Waters overlying this bank are strongly influenced by the generally cold Gulf of Maine waters on the north and warm oceanic waters on the south (Bigelow 1927). Due to relatively strong tidal and non-tidal water movements there is considerable mixing of water masses on and adjacent to Georges Bank.

In addition to the different water masses with their particular physical and chemical properties, the water depths and sediment types in the Georges Bank region are quite varied. Thus, a rather wide variety of habitats for marine organisms is available. This biotopic diversity is matched by the multifarious benthic forms.

Until recent years very little was known about the Georges Bank benthos. Occasional references to the occurrence of certain species appeared in some of the early taxonomic literature and faunal synopses (Gould 1870; Verrill, Smith, and Harger 1873). These reports were frequently based on specimens obtained from fishermen, a source of some of the earliest information about the fauna. First directed efforts toward a study of the benthos were dredgings made from the vessel *Bache* by Smith and Harger (1874). They reported on the species composition of a modest number of catches mainly from the eastern and northern parts of Georges Bank. These catches consisted principally of the larger, epi-benthic forms. The *Blake* made a few collections from the eastern and southern sections of the bank (Agassiz 1888). During the years 1882-1886 the two U. S. Fish Commission research vessels *Fish Hawk* and *Albatross* occupied a number of stations on Georges Bank where benthic faunal samples and hydrographic data were collected. Since that time, however, little has been added to our knowledge of the Georges Bank benthos until the past few years.

The investigation on which the remainder of this report is based was essentially a qualitative and quantitative survey of the benthic fauna on Georges Bank and adjacent areas. Special attention was given to geographic, bathymetric, and substrate relationships with the fauna. It is anticipated that a more complete and detailed analysis of this study will be published at a later date.

QUANTITATIVE SURVEY

Quantitative samples were collected from the research vessel *Albatross III* at 161 localities on and adjacent to Georges Bank in August 1957. The samples, which included both the sediment and fauna, were collected by means of a Smith-McIntyre (Smith and McIntyre 1954) grab sampler. A portion of sediment from each sample was saved for particle size composition and organic content analyses that were undertaken in the laboratory ashore. The remaining portion of each sample was washed through a sieve having 1-mm. apertures. Animals retained on the sieve were preserved in formalin for further processing ashore. After sorting and identification, the number of specimens and wet weight of each species or higher taxon were determined.

Faunal Components

The bulk of the Georges Bank benthic fauna was composed of four major taxonomic groups: Crustacea, Mollusca, Echinodermata, and Annelida. Other taxonomic groups present, but only in small quantities, were: Coelenterata, Ascidiacea, Bryozoa, Nemertea, Spiunculoidea, Porifera, Pycnogonida, Nematoda, and Brachiopoda. For convenience in referring to these last named categories, they have been combined under the heading Miscellaneous. A summary of the number of specimens and weight of each major component is listed in Table 1. The main aspects of faunal composition can be judged from this data.

TABLE 1. SUMMARY OF THE AVERAGE COMPOSITION OF GEORGES BANK BENTHIC FAUNA

Taxonomic group	Specimens (per m²) Number	Percentage	Wet weight gr/m²	Percentage
Crustacea	1113	66	8.2	5
Mollusca	54	3	64.6	41
Echinodermata	47	3	48.4	31
Annelida	334	20	9.2	6
Miscellaneous	142	8	26.2	17
Total	1690	100	156.6	100

As compared with the other faunal components the Crustacea were exceptionally abundant. However, in terms of weight they accounted for a smaller share than any other major group. The Amphipoda, which were very abundant and small in size, were the dominant crustacean group. The large numbers of specimens and small weights for Crustacea were primarily due to amphipods. Mollusca were very few in number but provided the greatest weight. The pelecypods contributed the main portion of this weight. Annelida were moderately numerous (334/m²), ranking second in number of specimens, but generally they were small-sized and formed a rather minor share in regard to weight. The Miscellaneous category contributed moderately

small numbers of specimens, and added significantly to the weight. Coelenterata and Ascidiacea were the main components of the Miscellaneous category.

Geographic Distribution

As previously stated, an inventory of the benthic fauna was one of the main objectives of this study. Inasmuch as the organisms that make up the benthos vary tremendously in quantity as well as in species composition from one locality to another, consideration of the geographic distribution is especially important. Both the number and weight of organisms per unit area are used in this discussion, but for most purposes weight is considerably more useful than number of specimens. Thus, the wet weight, expressed in grams per square meter of bottom, is most commonly used in this report.

The quantitative geographic distribution, by weight, of all benthic organisms, *i.e.*, all groups combined, is illustrated in Figure 1. Distinct differences in quantity were associated with geographic location. There were three areas where a high density (>100 gr/m²) of benthic animals occurred. These areas were located in the following sections

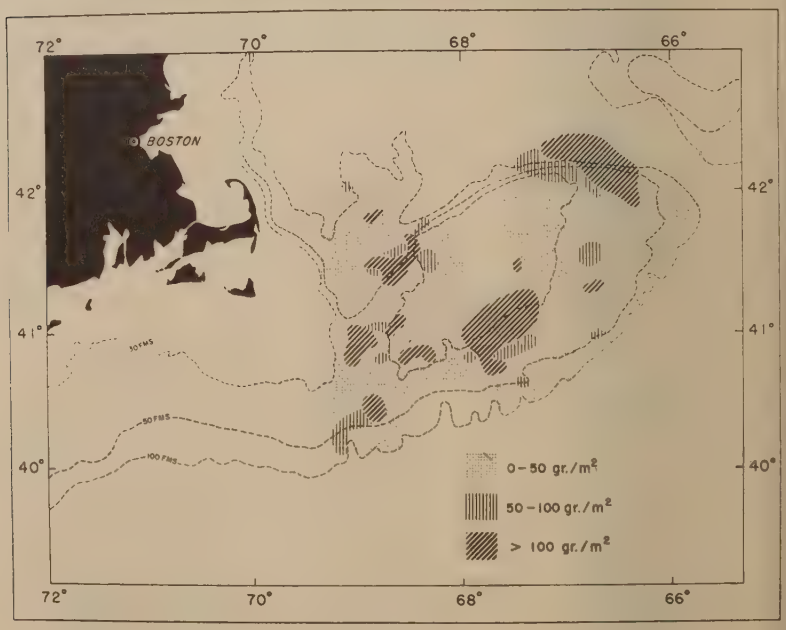

Figure 1. Geographic distribution of the benthos in terms of wet weight per m².

of Georges Bank: (1) northeast, (2) south-central, and (3) western. The first two of these areas each consist essentially of one large contiguous area, whereas the third is a cluster of six relatively small high-density patches that are considered as a single group for discussion purposes. Moderate densities (50-100 gr/m^2) of benthic animals were found adjacent to nearly all high-density areas. However, the total geographic area that supports a moderate density is distinctly more limited than that of either of the other two density categories. It is also apparent from Figure 1 that large portions of eastern and central Georges Bank, plus the deep-water basin to the northwest, support a rather small biomass ($<$50 gr/m^2).

Each major faunal component had a somewhat different and distinct geographic density pattern. Crustacea were most prevalent along the western and southeastern parts of the bank; moderate quantities occurred in the northeast and southern sections. Mollusca were most abundant on the northeast, south-central, and western portions of the study area. Echinodermata were especially dense in the central part of Georges Bank, with moderate quantities occurring on the bank's northeast, northwest, and south-central parts. Annelida were prevalent on the northeastern, south-central and western sections. They were the only group abundant in the deep-water basin northwest of Georges Bank.

Benthic Fauna and Bottom Sediments

Bottom sediments.—Bottom sediments on Georges Bank and adjacent areas are predominantly sands. Sediments in practically all sections of the study area contain sand, and it is the principal component in most sections. For comparison purposes, the sediments have been analyzed and classified according to standard procedures (Wigley 1961). The classification of sediment types used here is based on the system reported by Shepard (1953), using the four major size classes: gravel, sand, silt, and clay. Sediment categories, called textural classes, are named by one, two, or three size-class components depending upon the relative quantities in each sample. Most of these textural classes have binary names in which the predominant component plus the second ranking element are identified. A textural class name consisting of a single term is used when the sediment is composed of 75 percent or more of one size-class. Three terms are employed when each of three constituents make up 20 percent or more of the sediment.

The geographic distribution of textural classes in the study area is shown in Figure 2. Sand is the textural class that is overwhelmingly most widespread. It occurs over nearly all the central and southern

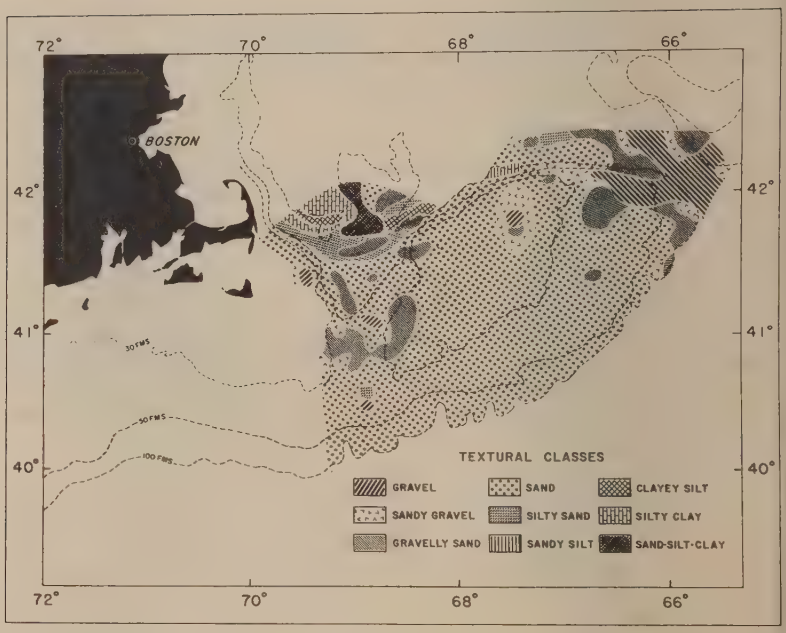

Figure 2. Geographic distribution of sediment textural classes in the Georges Bank region.

parts of the study area. Gravels, sandy gravel, and gravelly sand are found on the northeastern portion of Georges Bank. A few patches of these same classes also occur in the north-central and western sections. Fine-grained classes, mainly silty clay, sand-silt-clay, and silty sand, are found in the deep-water basin northwest of Georges Bank. A more comprehensive and detailed description of these sediments and methods of analysis are given by Wigley (1961).

Relationships between the fauna and sediment.—Striking correlations were observed between the type of bottom sediment and the quantity of benthic organisms. High abundance was associated with coarse sediments and low abundance was associated with fine sediments. In Figure 3 the mean number of specimens and mean wet weight of organisms are plotted for each textural class. The latter are arrayed in Figure 3 along the horizontal axis in decreasing particle size from left to right.

By far the greatest faunal weight was found in gravel and sandy gravel bottoms. The biomass in the sandy gravel sediment was exceptionally high (1300 gr/m^2), due largely to the occurrence of dense beds of *Modiolus modiolus,* the northern horse mussel. Moderate to

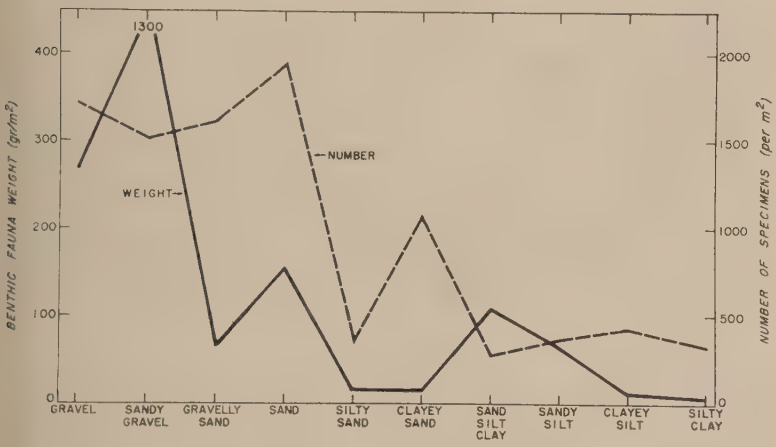

Figure 3. Mean number of specimens (per m²) and wet weight (gr/m²) in each textural class.

low quantities, 14 to 154 gr/m², occurred in sediments in which the sand fraction was dominant. Lowest weights were found in clayey silt and silty clay bottoms. These are the finest-grained sediments and the faunal weight occurring in these two textural classes was 11 and 7 gr/m², respectively.

The relation of numbers of specimens to sediment classes was quite similar to that for weight. Greatest numbers of specimens were found in gravels and sands; fewest specimens occurred in sediments containing large quantities of silt and clay. Organisms were most abundant (1934/m²) in the sand textural class. Gravel, sandy gravel, and gravelly sand also ranked high, with the number of specimens ranging from 1513 to 1718/m². Except for the clayey sand category, in which the number of specimens averaged 1074/m², the remaining textural classes (silty sand, sand-silt-clay, sandy silt, clayey silt, and silty clay) supported rather few specimens—255 to 436/m².

SUMMARY

In the New England coastal states fishing has been a major industry for over 300 years. A large segment of this industry is dependent upon the bottom-dwelling fishes, such as haddock, cod, hakes, and flounders. The principal source of nourishment for these species of fish is the benthic fauna.

The first quantitative inventory of the benthic fauna of a New England fishing bank was made in August 1957. The fauna was found to be composed (by weight) of the following groups: Mollusca

41%, Echinodermata 31%, Miscellaneous groups 17%, Annelida 6%, and Crustacea 5%. The over-all average weight of the benthic fauna was 156.6 gr/m^2; average number of specimens was 1690/m^2.

Pronounced differences in quantity and species composition of the benthic fauna were associated with geographic location. The fauna was most plentiful on the (1) northeast, (2) south-central, and (3) western sections of Georges Bank. The benthic fauna also showed marked differences in kind and quantity in relation to bottom sediments. The richest fauna (268 to 1300 gr/m^2) occurred in the coarse-grained sediments, such as gravels and sandy gravel. Fine-grained sediments (clayey silt and silty sand) yielded the smallest biomass, 7 to 11 gr/m^2.

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DISCUSSION

DISCUSSION LEADER CHAPMAN: The beginning of marine ecology is just now with us. I don't think there has been any quantity of work of this nature done outside of the North Sea, and I'm tremendously interested in the complex problems of 300 or 400 different species of organisms and their inter-relationships. I think you're going to be an elderly man before you get them worked out.

MR. JOHN SIMPSON [Omaha, Nebraska]: What is the comparative area of the Georgia Banks?

MR. WIGLEY: We usually take the 100-fathom depth contour as the outline of the Bank, and the total area encompassed is approximately 12,000 square miles. It is quite a large area.

MR. SIMPSON: Is it an irregular sized area? Approximately how many miles by how many miles?

MR. WIGLEY: It is 150 miles long and 75 miles wide.

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AN APPLICATION OF RADIOACTIVE ISOTOPES IN FISH TAGGING

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One of the major voids in the knowledge of Alaska herring (Clupea harengus pallasi) is lack of information on the number, size, extent, and utilization of discrete stocks. To obtain this information, studies on methods of discriminating among herring races were inaugurated four years ago along several distinct lines by the Bureau of Commercial Fisheries, Alaska Region. In part the approaches taken involve: (1) assessment of separate spawning stocks to determine the number of discrete spawning populations; (2) studies of size, weight, and sex composition of herring taken by the reduction fishery as a means of detecting the presence of separate populations and their extent of intermingling in the fishery; (3) comparison of growth increments (after the mathematical adjustment for temperature effects) exhibited by the various stocks of herring taken by the reduction fishery, also to detect separate populations; (4) preliminary study of herring blood to determine the applicability of serological methods to herring racial analysis; (5) study of morphological features of numerous groups of herring, using the distance function concept of Rao, to determine the number and extent of utilization of various races; and (6) study of the nature, movement, and migration of individual herring schools as a means of understanding population intermingling and mixing.

All of these approaches have provided, or show evidence of being able to provide, useful information on the number and extent of separate herring populations in Alaskan waters. However, none of them provide all the parameters necessary for an adequate examination of population dynamics. These data can be obtained only through a tagging program. Therefore, in 1956, the means and methods of conducting a tagging program on a pelagic fish such as herring were explored.

A review of the problem indicated that: (1) an internal tag would be easiest to apply and to detect, (2) a tag detection device would be required that would operate at extreme low levels of sensitivity, and (3) a tagged fish ejector must be developed that would operate without impeding plant operations.

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Some of the considerations involved in reaching these conclusions may be of interest.

Bulk handling of herring in western North America precludes the use of an external tagging technique based on visual detection. Regardless of high individual visibility, external tags would pass virtually undetected through the present herring processing plants. Previous work in Alaska and Canada has shown the ease with which internal tags might be inserted into herring and the relatively low mortality rate brought about by internal tagging as opposed to external tagging.

The nature of the tag detector involves consideration of the type of tag employed. The metallic or magnetic tag has been proven effective in both herring and pilchard investigations along the West Coast. However, investigators using either type of tag recognize that the magnetic and metal detectors miss a percentage (often large) of tagged fish. Even a safety magnet, located in a powdered-meal line occasionally is blocked by a sufficient thickness of meal so that tags are lost. More important, all tags that are collected on the magnet at the end of a production line have lost much of their potential usefulness, since there is no way of determining from what fish or group of fish they originated. The present widespread use of electrical machinery in reduction plants greatly increases the electronic filtering problems and difficulty of maintaining electronic balance circuits in magnetic or metallic detection equipment.

Electronically, several different methods are available by which metallic and magnetic tags can be detected under more or less ideal or laboratory conditions. The cost of developing improved circuitry to assure a greater percentage tag recovery is prohibitively high. In all probability, these more sophisticated circuits would require more skillful technicians and more consistent maintenance in the field than is usually feasible. Consequently, development of a new means of detecting an internal tag was a necessity.

Correspondingly, independent development of a fish ejector that would respond to input signals from any type of detecting device was required. A second requirement was that the ejector should isolate only the specimen or specimens containing tags. Equipment previously employed for use with internal metal tags would eject up to two dozen fish at a time, and it was often

necessary to dissect specimens to locate one containing a tag. Finally, ejection gear was not to interfere or delay normal processing techniques at reduction plants.

Of the many methods considered for the detecting of internal tags, several were rejected because their use was impractical under Alaskan field conditions and/or because of their high cost of operation and maintenance. The only promising technique of detecting a tag in herring when it was screened by a mass of fish, slime, and water was the employment of a radioactive tag. Radioisotopes have been tried for fish tagging under laboratory conditions, and at least one worker suggested the use of a radioactive fish tag for field use. The survey of the problem by Seymour[2], however, indicated that for most applications the use of radioisotopes for tagging was not feasible. The single exception was for the type of operation used in taking herring and similar fishes for reduction.

After a careful survey on the basis of technological grounds, safety considerations, and a cost basis, the use of the radioactive techniques was chosen as most likely to succeed.

The construction of the necessary equipment proposed by our group was carried out by the Fisheries Instrumentation Laboratory, Bureau of Commercial Fisheries, Seattle, Washington. To a great degree the technical competence of Richard vanHaagen and Richard Othberg made the engineering system which we advanced a working practicality.

Description of Equipment

Essentially, the units of the system may be described as follows. The tags themselves are made of Alnico V magnetic rods one-half inch long and one-eighth inch in diameter. Alnico V was chosen because it is the strongest permanent magnet known and because of its cobalt content. The tags are gold-flashed and labeled radioactive. Each bears a serial number and directions for return, should it fall into the hands of a member of the general public. Finally, the tag is coated with transparent polyethylene and sealed to insure inertness in the herring and in sea water. The tags are irradiated at one of the National Laboratories to the very low level required for detection by the newly designed sensitive

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2. A. H. Seymour, Proc. Gulf and Caribbean Fisheries Institute, 10th Sess. (1957), 118.

equipment. Gamma emission from Cobalt 60 at a level of 10 microcuries would fall well within safety requirements and would remain within a level to assure detection even if the tag was shielded by a mass of other fish and debris. Preliminary studies have shown this level of radiation can be borne by herring without harm.

Tags are packaged in plastic cartridges to facilitate identification and handling efficiency.

Tag injection equipment has been designed and fabricated to insert the tag into the abdominal cavity of the fish. Narcoticized herring (to reduce mortality from handling) are impaled on the injector, and pressure from a foot pedal gently inserts a tag into the peritoneal cavity. At the time the tag is inserted, an antibiotic is sprayed over the tag and over the wound to reduce the possibility of infection.[3]

Tagged herring are recovered from the commercial catch in reduction plants. The tag detector consists of a radiation detector and associated electronic circuits. The detector unit is relatively unsophisticated, except for the "fail-safe" features of the circuit. The detection unit provides a signal to operate the tagged fish ejector at the proper instant. The detector can operate separately from the ejector, but in our application the two units are combined.

The detection and ejection of tagged fish may best be accomplished as the fish enter the processing plant. Because the detection equipment is an integral part of the unloading conveyor system, it was designed to eject fish with a minimum of delay to the processing machinery. This in itself is a significant advance in that plant operators appear to offer less objection to installation of units into the production lines than the old metal detectors. It is to be recalled that reduction plants participate in any tagging program wholly on a voluntary basis. As herring are unloaded, they pass through the plant's weighing machine and thence onto the tagged fish detector and ejector. In essence, the detector and ejector units appear to be part of the conveyor belt. Radiation from any and all tagged fish is picked up by a scintillation detector at the head of the ejector; in a fraction of a second the machine comes to a stop; in a second fraction of a second, the tagged fish and all fish in the immediate neighborhood are ejected from the main conveyor belt, and in a third fraction of a second, the machinery is again in

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3. Present incomplete experiments suggest that this precautionary feature may not be necessary.

operation at full speed--the total elapsed time being less than three seconds. With this schedule, ejection will not in any way impede plant operations. The ejected fish are picked up individually by a small conveyor belt, and each is examined for radioactivity. The tagged fish are diverted into a separate receptacle, and all remaining fish are dropped back on the main conveyor line at the head of the ejector. Thus, the fish are checked for radioactivity a second time as they pass the radiation counter. One hundred percent efficiency of tag detection is assured through this technique. High safety factors and "fail-safe" techniques are built into the machinery. A third detector is located at the terminal end of the ejector and would halt the equipment should any breakdown allow tags to pass the first detection stage.

Safety Provisions

Additional safety measures have been taken to prevent any radioactive tag from reaching the finished meal product.

The magnetic nature of the tag insures retention even if through some unlikely and nearly impossible chance a tag should pass through the ejector equipment undetected. The tag itself would magnetically attach to the first piece of metallic machinery it contacts. Even if it were ground to a powder, each particle would become a new magnet, and the metallic dust would be retained on plant machinery rather than enter the meal. The metal detector, which is a part of the plant's debris straining equipment, would pick out any minute particles of the tag that might reach the end of the meal line. To assure safety and to alleviate possible criticisms from the consumer, the meal product will be checked with radiation survey meters. To recover tags that may be lost from rotting fish, the holds of herring fishing vessels will be examined with survey meters at frequent intervals.

There is relatively little possibility that any person in the general public will come in contact with a tagged herring. The meal produced by the reduction operation is used in high protein poultry feeds, and the oil is used in paints, cosmetics, and ore flotation processes. The chances of obtaining a tagged herring in a catch of bait are extremely small. Should this occur, however, the danger from exposure to radiation would be negligible. The prospect of anyone swallowing a tag in a pickled herring is even smaller. If the tag were not discarded in gibbing the fish, the sealed nature of the tag

itself insures that, if it were not discovered in chewing, it would pass intact through the digestive system, giving a negligible dose of radiation to the digestive tract. Several tags would have to be dissolved in the body fluid before the radiation level in the liver (the organ which accumulates cobalt faster than others) would reach a dangerous point--a most unlikely circumstance.

Further evidence of the inherent safety of the tag and of the low levels of radiation employed are the simplified shipping and storage procedures prescribed by government regulations. Egg crate cartons containing tags are acceptable for shipment through the U. S. Mail.

To monitor radiation effects on personnel participating in the tagging program, film badges will be worn. Personnel using the injection equipment will also wear adhesive thumb-type badges.

Field Operation

Naturally any widespread use of radioactive materials is of concern to the general public. Our proposed use of radioactive tags was made known to the public, processors, wholesalers, and health agencies. As the use of radioactive materials was to conform to Atomic Energy Commission specifications, no objections to our application were registered. In February, 1960, the AEC granted a license for the employment of our technique.

Installation of detection and ejection equipment at the three operating plants in southeastern Alaska was completed by early summer. Field use of the equipment pointed out some shortcomings which were relatively easy to rectify. The major problems involved modifying existing plant features to accomodate our equipment. A limited number of herring were tagged and released during the summer of 1960, and by the end of the fishing season, some recoveries were made. Final evaluation of the technique must await at least one additional year of field operations.

Summary

Study of the structure of Alaska herring populations is one of the major efforts of the Marine Fisheries Investigations, of the Bureau of Commercial Fisheries in Alaska. Certain aspects

of this study can only be accomplished through a tagging program. Use of internal tags has been successfully applied to pelagic fish such as herring. Efficient recovery of tagged fish has been a major problem. A research and development program designed to perfect a better tag detecting system resulted in the design of a radioactive magnetic tag, tag injection equipment, and associated detection and ejection machinery. The equipment has been designed to detect radioactive tags at high speeds and under heavy radiation masking conditions with 100 percent efficiency. The system costs a fraction of that required to fabricate less efficient magnetic and metallic detectors. Appropriate safety features are an integral part of the system, which has been granted an AEC license. The technique is currently undergoing field evaluation in southeastern Alaska.

SURVIVAL OF PINK SALMON AT LITTLE PORT WALTER RESEARCH STATION

T. R. Merrell, U. S. Fish & Wildlife Service
Bureau of Commercial Fisheries, Juneau, Alaska

Little Port Walter is a research station operated by the Bureau of Commercial Fisheries to study pink salmon biology. In most recent years, pink salmon have comprised the major part of Alaska's commercial fishery harvest, and it is vitally important that factors controlling their abundance be known. Despite many years of study in Alaska, British Columbia, and Washington, the interaction of these controlling factors is only beginning to be understood.

Two of these factors which seem to be important in the early freshwater life history of pink salmon at Little Port Walter are: time of spawning, and stream gradient and its association with survival.

Little Port Walter is located on Sashin Creek at the southern end of Baranof Island, southeastern Alaska, about 60 miles south of Sitka. This location was selected for studying pink salmon mainly because it is on the very edge of the commercial fishery, minimizing the complicating effects of a fishery on marine survival.

Adult pink salmon have been counted at a weir at Little Port Walter annually since 1934, and seaward migrating fry have been counted each spring since 1940. These counts provide the longest continuous record of pink salmon production on the Pacific Coast. Other data that have been recorded and analyzed include air and water temperatures in the stream and in the gravel, rainfall and stream discharge, and length-weight, sex, and fecundity of adult salmon.

Freshwater Survival

Little Port Walter environmental conditions do not fluctuate widely and do not seem to be a major cause of fluctuations in survival. We have been unable to demonstrate any consistent relationship between survival of eggs and fry and air or water temperature, or even rainfall, although some mortality is evident during extreme floods. There is also little evidence that predators in the stream are an important factor.

The only factor that has consistently affected survival is time of spawning. This relationship of spawning time to survival of fry was first report by Skud in a paper that appeared in Copeia in 1958. His conclusions were based on data through 1955; since then, five more years of data have conclusively shown that survival is invariably greater when spawning is early. Furthermore, since 1950, the odd-year runs have always been earlier than the even-year runs. Thus, highest survival occurs every other year. Between 1950 and 1959, the dates on which 50 percent of the run passed the weir were, on the average, 12 days earlier for odd-year runs than for even-year runs (September 1 and 13). The most probable reason for higher survival from earlier runs is that water temperatures are dropping during this season, and eggs get a head start in development before cold winter weather retards development. Laboratory experiments have shown that the most vital and sensitive period of development is immediately after fertilization. In the even years, when eggs are deposited later in the season, they do not reach an advanced stage of development before the onset of cold weather and are thus more sensitive to environmental conditions.

In the fall of 1959, an unprecedented large run of pink salmon totaling 35,000 returned to Little Port Walter, the largest run since 1942. Several factors combined to produce this large run: the 1957 parent run spawned earlier than any other run in the station's history, which coincided with a

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GRAY WHALE OBSERVATIONS

Along the Pacific coast of California, Oregon and Washington where it often migrates close to shore and enters very shallow water in bays and lagoons, the gray whale, *Eschrichtius glaucus*, recently believed to be nearly extinct, is now familiar to more people than any other large whale. At La Jolla, California, viewing gray whales from excursion vessels has become a popular tourist attraction. However, the migratory route of the gray whale in northern waters and its distribution in summer is little known. Observations of gray whales made by employees of the Bureau of Commercial Fisheries' Marine Mammal Research office, from research vessels, are made available here to assist in filling in the incomplete parts of the distribution pattern.

Observations off Washington.—Gray whales in northward migration were sighted off the Washington coast, 24 and 25 April 1959, by the U. S. Fish and Wildlife Service charter vessel M/V "Tacoma."

On 24 April, a few gray whales were seen off Cape Johnson (47° 58′ N; 124° 41′ W). One of the lookouts aboard the vessel reported an object breaking and partially clearing the water about 7 miles west of Cape Johnson. Upon investigation, the object proved to be a dead gray whale. The whale was in a bloated condition, the penis and penis sheath had been extruded, and the intestines had been forced from the body and were floating separately about 50 feet distant from it.

During the afternoon of 24 April, over 200 gray whales were seen between Destruction Island (47° 40′ N; 124° 29′ W) and James Island (47° 54′ N; 124° 39′ W), a distance of 15 miles. The whales were in water 20–50 fathoms in depth and were about 5–15 miles offshore. They were observed in singles, pairs and groups of 3–4. The general movement was northerly although, when observed, some were resting and others were feeding and playing. One whale was observed near a 2 × 12 in. plank. The whale came up near the plank several times and either hit or held it with its flipper.

On 25 April, the vessel ran directly offshore from the anchorage at James Island. Gray whales were seen to the north and south of the course and were numerous from the buoy at a depth of 20 fathoms out to about 9 miles offshore at a depth of 50 fathoms.

Observations off Alaska.—Ichihara (Sci. Repts. Whales Res. Inst., 13: 201–205, 1958), in reporting three groups of gray whales consisting of 2, about 20, and about 150 individuals seen west and north of St. Lawrence Island in August 1955, proposed a migration route for the gray whale which entered the eastern Aleutian passes and crossed the central Bering Sea. This was considerably east of the route proposed by Gilmore (Sci. Amer., 192: 62–67, 1955).

On 11 May 1957, eight gray whales in scattered pairs were seen moving toward Narrow Cape between Kodiak and Ugak Islands. The whales were in very close to the kelp beds along Kodiak Islands. The location of these whales suggests that their migration route might lead past the islands off the Alaska Peninsula and follow the route into the Bering Sea proposed by Ichihara (*op. cit.*).

From the Exploratory Fisheries vessel "John N. Cobb," engaged in biological investigations, on 10 August 1959, at 67° 10′ N and 166° 43′ W in the Chukchi Sea, an estimated 100 gray whales were seen feeding over several square miles of ocean. The water depth was about 24 fathoms. The whales made a large muddy blotch in the water as they came to the surface to blow. It seems apparent that in feeding along the bottom the whales gathered mud along with food and were expelling it through their baleen as they rose to the surface. The sticky, clay mud making up the bottom of much of the eastern Chukchi Sea is difficult to wash out. Although the short, coarsely fringed baleen of the gray whale is well adapted for sifting mud from food items, it would be of interest to know if the gray whale swallows some mud along with its food. According to Arseniev and Zenkovich (*in* Kleinenberg and Makarov, Trans. USSR Inst. Fish. & Oceanog., Moscow, 1955) gray whales feed on bottom-living amphipods in the Chukchi Sea. No direction of movement

was evident in this group of whales; they were headed in various directions as they rose to the surface.

On 16 August, observers on the University of Washington oceanographic vessel "Brown Bear" observed about 100 gray whales at 67° 25′ N and 167° 06′ W, feeding in the same manner as described above.

On 19 August, two gray whales were seen from the "John N. Cobb" feeding near 67° 40′ N and 167° 12′ W; and on 20 August, three others, also feeding, were seen at 67° 57′ N and 168° 02′ W. On 29 August, about 20 gray whales, widely scattered and traveling generally southward, were observed at 67° 18′ N and 166° 30′ W. Some of the whales in this group were moving in pairs. None of the muddy water areas associated with feeding was noticed.

Surface-water temperatures ranged from 46.2 to 49°F where whales were observed feeding. Bottom temperatures were 37 to 38°F.

Northern phalaropes (*Lobipes lobatus*), kittiwakes (*Rissa tridactyla*) and arctic terns (*Sterna paradisaea*) followed the feeding whales, settling into the muddy spots where the whales had come to the surface. Whales observed on 19 and 20 August were accompanied by slender-billed shearwaters (*Puffinus tenuirostris*) as well as the birds listed above.

A gray whale, 43 feet in length, had drifted ashore at Cape Thompson in early August. Two others were reported on the beach in the vicinity. On 29 August, a dead gray whale was found drifting about 50 miles west of Kivalina village. It was not greatly bloated. The cause of death of these whales is unknown.—Ford Wilke and Clifford H. Fiscus, *Bureau of Commercial Fisheries, Fish and Wildlife Service, Seattle 15, Washington.* *Received 8 December 1959.*

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AGE AND LENGTH COMPOSITION OF THE SARDINE CATCH OFF THE PACIFIC COAST OF THE UNITED STATES AND MEXICO IN 1958-59[1]

ROBERT S. WOLF, U. S. Bureau of Commercial Fisheries, and
ANITA E. DAUGHERTY, Marine Resources Operations,
California Department of Fish and Game

INTRODUCTION

This is the thirteenth report on age and length composition of the catch of California sardines (*Sardinops caerulea*) off the Pacific coast of North America. These reports have been prepared on a seasonal basis since 1941-42.

Previous to the 1957-58 report (Daugherty and Wolf, 1960), this series was devoted almost entirely to presenting basic age and length data of the seasonal catch of the sardine fishery. Beginning with the above mentioned report a more comprehensive picture of the fishery has been presented.

The assistance of Leighton G. Claussen, formerly of the U.S. Bureau of Commercial Fisheries, and of Doyle Gates of the California Department of Fish and Game is gratefully acknowledged.

THE FISHERY

During the 1958-59 season 102,621 tons of sardines were landed in central and southern California. This was the largest seasonal catch there since 1951-52 when 127,000 tons were caught. It is possible that sardines were more plentiful than in recent years and that except for economic limitations[2] the landings might have exceeded the 1951-52 level.

Central California

In the central California region, which lies north of Point Arguello, the sardine season opened on August 1, 1958. During the first dark-of-the-moon period, "August",[3] 4,599 tons of sardines were landed. This was the first major catch of sardines in the region since the more than 15,700 tons landed there during the 1951-52 season. During "September" another 9,174 tons of sardines were taken. In "October" 5,450 tons were caught, and in "November" 2,917 tons. In "December" 2,460 tons were landed and in "January" 14 tons, which brought the total for central California to 24,614 tons for the season which ended on January 1, 1959.

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[1] Submitted for publication December 1960.
[2] See pages 274 and 275 for information on limits.
[3] Lunar months are always referred to in quotation marks to distinguish them from the calendar months they approximate. Calendar dates for lunar months during 1958 are presented in Table 1.

Central California fishermen were paid $60 per ton for their fish at the beginning of the season. Where necessary, however, they were obliged to pay the charges of transporting the fish to the cannery. After "September" and for the remainder of the season, the price paid was $50 per ton, still exclusive of trucking charges.

Thirty boats were involved in the central California sardine fishery. These included 13 large purse seiners (60 ft. or over), 4 small purse seiners, and 13 lampara boats. They were on nightly cannery-imposed limits of 35-40 tons. On some nights no limits were set.

Approximately two-thirds of the total tonnage was landed at either Morro Bay or Avila and trucked to processors in Monterey or San Francisco. The remainder of the catch was landed at Monterey Bay plants. There were seven cannery plants in operation: five in Monterey proper, one in Moss Landing, and one in San Francisco. Approximately 3,300 tons of sardines were processed in San Francisco and 21,300 tons in the Monterey Bay area.

Southern California

The sardine season in southern California opened on September 1, 1958, and closed coincident with the central California season on January 1, 1959. This fishing region includes the waters between Point Arguello and the Mexican border.

During the season, 78,007 tons of sardines were landed in the southern California region—72,932 in the Los Angeles-Long Beach area. At Port Hueneme 5,075 tons were landed, of which 4,429 tons were trucked to a cannery at nearby Oxnard or to the canneries of the Los Angeles-Long Beach area. The remaining 646 tons were trucked north to the Monterey Bay area. During "September" 25,677 tons of sardines were landed in southern California, in "October" 29,972 tons, in "November" 16,470, in "December" 5,731, and in the first and only week of the "January" dark (which commenced on December 25) 157 tons.

Southern California fishermen, like those in central California, received $60 per ton during "September". When fishing resumed in "October" the price was renegotiated at $50 per ton where it remained until the end of the season.

The fleet in southern California consisted of 119 boats: 67 large purse seiners, 16 small purse seiners, and 36 lamparas. In recent years the number of large purse-seine vessels has decreased through the loss of some and the sale of others.

Throughout the season sardines remained in the vicinity of Santa Rosa, Santa Cruz and Anacapa Islands. The major part of the southern California catch came from this area, although some fish were taken along the adjacent mainland shore and as far east as Malibu Beach. This season differed from most recent ones in that fishing operations did not extend appreciably towards the Mexican border.

During "September" southern California boats were on individual nightly catch limits up to 100 tons. Before fishing resumed in "October" processors agreed to take a minimum of 40,000 tons during the remainder of the season concurrent with the ex-vessel price drop

This was in addition to the 25,677 tons already landed. Each boat was guaranteed a minimum nightly catch limit of 40 tons until the 40,000 tons were landed. Nightly limits held at 40 to 50 tons until the middle of "November" when the 40,000-ton quota was achieved. From then until the end of the season, nightly limits ranged from 20 to 40 tons.

FIGURE 1. Upper Baja California showing sardine fishing areas (shaded) and ports of landing. Statistical subareas for the Ensenada fishery are superposed (taken from Oficina de Cartografia, Julio de 1954).

Weather conditions during the season were considered good. Except for the usual fog, and a bad storm the night of November 14 resulting in the loss of one lampara boat, no great amount of time was lost due to weather.

Baja California

To augment information obtained from sampling California landings, the sampling program in Baja California, Mexico, was considerably expanded in 1957. In 1958-59 sardine landings were sampled at Ensenada, San Quintin and Cedros Island (Figure 1).

Sardines are taken commercially throughout the year in upper Baja California. In 1958 the total catch in Baja California was 19,383 tons. Of these, 7,793 tons were taken during the period of the California fishery and 11,590 tons during the interseason. Baja California fishermen received an ex-vessel price equivalent to $40 in U. S. currency per ton for their sardines. In cases where the canner supplied fuel for the boat the price was $30.

Currently there are about 30 boats in the Baja California fishery, but the number varies according to the abundance of pelagic species and market conditions. Contrary to the situation in California, the jack and Pacific mackerels are preferred species when they are available. When fishing becomes an unprofitable venture, the boats may be used in other pursuits or may be tied up.

Ensenada, located 60 miles below the U. S.-Mexico border, is the largest fishing port in Baja California. Five canneries there processed sardines. These were supplied by boats that operated between Los Coronados Islands and Cape Colnett. The cannery at San Quintin was supplied by one or two boats operating in and around San Quintin Bay. A cannery at Cedros Island was supplied by three to six boats that operated between northern Sebastian Vizcaino Bay and Turtle Bay.

No information is available as to whether nightly catch limits are ever imposed on Baja California fishermen.

TABLE 1

Calendar Dates of Lunar Months During 1958

Lunar month	Lunar period[1]	Dates	Lunar month	Lunar period	Dates
"January"	473	January 5-February 3	"August"	480	July 31-August 29
"February"	474	February 4-March 4	"September"	481	August 30-September 27
"March"	475	March 5-April 3	"October"	482	September 28-October 26
"April"	476	April 4-May 3	"November"	483	October 27-November 25
"May"	477	May 4-June 1	"December"	484	November 26-December 24
"June"	478	June 2-July 1	"January"	485	December 25-January 23[2]
"July"	479	July 2-July 30			

[1] Lunar periods have been numbered serially since "November" of the 1919-20 season.
[2] All commercial sardine fishing ceased on December 31.

AGE AND LENGTH COMPOSITION

In central California all but five of the 716 fish aged were one to three years old. Lengths ranged between 166 and 248 mm. standard length (Table 2). Eight age groups were separated in the 1,044 fish, 166 to 252 mm. in standard length, from southern California (Table 3). A total of 958 fish were aged from Baja California samples during

TABLE 2

Length Composition of Year-classes in Sardine Samples from the Central California Commercial Catch, 1958-59 Season

Age	0	1	2	3	4	5	6	
Year class	1958	1957	1956	1955	1954	1953	1952	Total
Standard length mm.								
166	--	--	1	--	--	--	--	1
168	--	--	--	--	--	--	--	--
170	--	1	8	--	--	--	--	9
172	--	5	7	--	--	--	--	12
174	--	5	23	1	--	--	--	29
176	--	10	29	2	--	--	--	41
178	--	9	40	2	--	--	--	51
180	--	17	65	10	--	--	--	92
182	--	13	47	14	--	--	--	74
184	--	10	73	19	--	--	--	102
186	--	8	63	16	--	--	--	87
188	--	2	48	16	1	--	--	67
190	--	1	44	18	--	--	--	63
192	--	2	28	10	--	--	--	40
194	--	1	12	10	--	--	--	23
196	--	--	5	7	--	--	--	12
198	--	--	4	3	1	--	--	8
200	--	--	1	--	--	--	--	1
202	--	--	--	--	--	--	--	--
204	--	--	1	--	--	--	--	1
206	--	--	--	--	1	--	--	1
236	--	--	--	--	--	--	1	1
248	--	--	--	--	1	--	--	1
Totals	--	84	499	128	4	--	1	716
Mean lengths	--	181	184	187	210	--	--	184

the period that corresponded to the California fishery. The age range was one through five, and the length range was 110-206 mm. (Table 4). In Baja California interseason six year-classes were represented in the catch. Because the annulus was formed during this period with an accompanying age change, these fish were tabulated by year-class only. A length range of 118-232 mm. was observed from 696 fish (Table 5). Mean lengths at each age are also shown in the tables.

Length and age compositions by year-class are shown by lunar month for each region in Figure 2. Although length composition during the regular season differed among regions, it remained fairly stable within

TABLE 3

Length Composition of Year-classes in Sardine Samples from the Southern California Commercial Catch, 1958-59 Season

Age	0	1	2	3	4	5	6	7	8	9	
Year class	1958	1957	1956	1955	1954	1953	1952	1951	1950	1949	Total
Standard length mm.											
166	--	1	--	--	--	--	--	--	--	--	1
168	--	--	3	--	--	--	--	--	--	--	3
170	--	--	--	--	--	--	--	--	--	--	--
172	--	5	3	--	--	--	--	--	--	--	8
174	--	5	3	2	--	--	--	--	--	--	10
176	--	4	9	--	--	--	--	--	--	--	13
178	--	4	16	--	--	--	--	--	--	--	20
180	--	10	27	5	--	--	--	--	--	--	42
182	--	9	36	8	--	--	--	--	--	--	53
184	--	12	40	11	1	--	--	--	--	--	64
186	--	10	47	10	--	--	--	--	--	--	67
188	--	8	58	12	--	--	--	--	--	--	78
190	--	8	74	19	1	--	--	--	--	--	102
192	--	6	61	17	3	--	--	--	--	--	87
194	--	3	53	32	2	--	--	--	--	--	90
196	--	5	42	18	1	--	--	--	--	--	66
198	--	4	39	16	--	--	--	--	--	--	59
200	--	2	24	22	--	1	--	--	--	--	49
202	--	1	19	13	1	--	--	--	--	--	34
204	--	3	24	10	3	--	--	--	--	--	40
206	--	1	13	7	1	--	--	--	--	--	22
208	--	3	7	6	--	--	--	--	--	--	16
210	--	--	6	8	4	1	--	--	--	--	19
212	--	--	6	2	5	--	--	--	--	--	13
214	--	--	3	2	3	3	--	--	--	--	11
216	--	--	2	4	3	1	1	--	--	--	11
218	--	--	1	2	2	--	--	1	--	--	6
220	--	--	1	1	--	--	--	--	--	--	2
222	--	--	--	3	--	1	--	--	--	--	4
224	--	--	--	--	3	1	1	--	--	--	5
226	--	--	--	1	2	1	1	--	--	--	5
228	--	--	--	2	1	2	1	--	--	--	6
230	--	--	--	1	2	4	--	--	--	1	8
232	--	--	--	1	--	--	--	--	--	--	1
234	--	--	--	2	1	--	--	--	--	--	3
236	--	--	--	--	1	--	1	--	--	--	2
238	--	--	--	1	1	--	1	--	--	--	3
240	--	--	--	--	3	3	1	--	--	--	7
242	--	--	--	--	1	1	2	--	--	--	4
244	--	--	--	--	1	--	1	--	--	--	2
246	--	--	--	--	1	--	3	--	--	--	4
248	--	--	--	--	--	1	--	1	--	--	2
250	--	--	--	--	--	--	--	--	--	--	--
252	--	--	--	--	1	1	--	--	--	--	2
Totals	--	104	617	238	48	21	13	2	--	1	1044
Mean lengths	--	187	191	197	216	227	237	233	--	230	195

them. The only major change occured in southern California where the size range decreased from 160-255 in "September" to 165-220 in "December". The 1956 class dominated in all regions during these months, and it is obvious from inspection that variations in the length curves are matched by similar variations in year-class composition.

TABLE 4

Length Composition of Year-classes in Sardine Samples from the Baja California Commercial Catch, 1958-1959 Season ("September" through "December")

Age	0	1	2	3	4	5	
Year class	1958	1957	1956	1955	1954	1953	Total
Standard length mm.							
110	--	--	1	--	--	--	1
130	--	1	--	--	--	--	1
132	--	--	--	--	--	--	--
134	--	--	--	--	--	--	--
136	--	--	1	--	--	--	1
138	--	--	3	--	--	--	3
140	--	1	6	1	--	--	8
142	--	3	7	--	--	--	10
144	--	3	14	1	--	--	18
146	--	2	15	--	--	--	17
148	--	11	25	3	--	--	39
150	--	11	39	2	--	--	52
152	--	7	64	2	--	--	73
154	--	11	58	7	--	--	76
156	--	12	61	5	--	--	78
158	--	11	82	--	--	--	93
160	--	7	59	9	--	--	75
162	--	8	82	10	--	--	100
164	--	4	53	9	--	--	66
166	--	3	36	4	--	--	43
168	--	1	47	5	--	--	53
170	--	4	21	3	--	--	28
172	--	2	16	--	--	--	18
174	--	2	10	3	--	--	15
176	--	1	12	3	--	--	16
178	--	--	6	2	--	--	8
180	--	--	10	4	--	--	14
182	--	--	3	3	1	--	7
184	--	--	3	5	--	--	8
186	--	--	3	2	--	--	5
188	--	--	1	2	2	--	5
190	--	--	3	4	--	--	7
192	--	--	--	6	--	1	7
194	--	--	1	--	1	--	2
196	--	--	--	--	3	1	4
198	--	--	--	2	--	--	2
200	--	--	--	3	--	--	3
202	--	--	--	--	1	--	1
204	--	--	--	--	--	--	--
206	--	--	--	--	1	--	1
208	--	--	--	--	--	--	--
Totals	--	105	742	100	9	2	958
Mean lengths	--	156	160	170	194	194	161

During the Baja California interseason length composition was more varied. The primary modes shifted from 125 mm. in "February" and "March" to 190 mm. in "April" and "May". It went down to 170 mm. in "June" and "July", then up to 180 mm. in "August". Again the variations in length composition were reflected in differences in year-class composition. All months of the interseason were dominated by the 1956 class except "April" and "May", when the 1955 class was dominant.

Lunar month summaries of the year-class composition of catch samples were used to obtain the year-class composition of the total catch.

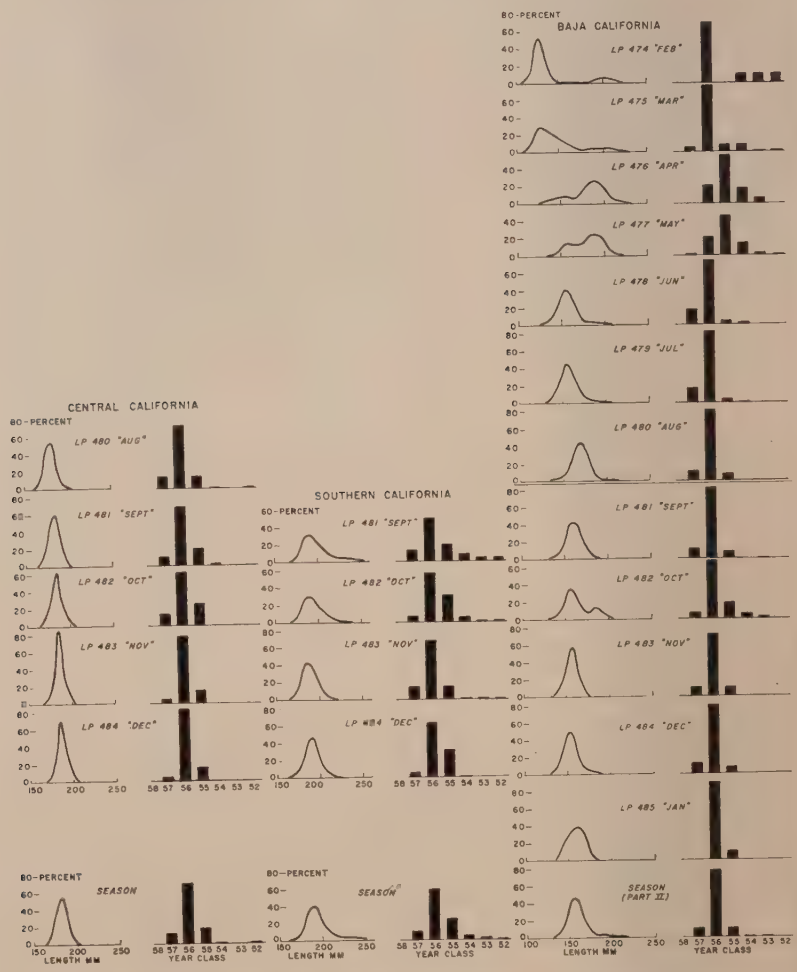

FIGURE 2. Percentage length and year-class composition of all samples of the 1958-59 commercial sardine catch. Length data are summarized by 10 mm. intervals.

TABLE 5

Length Composition of Year-classes in Sardine Samples from the Baja California Interseason Catch ("January"-"August")

Year class	1958	1957	1956	1955	1954	1953	1952	Total
Standard length mm.								
118	--	--	1	--	--	--	--	1
120	--	--	4	--	--	--	--	4
122	--	--	4	--	--	--	--	4
124	--	1	11	--	--	--	--	12
126	--	--	12	--	--	--	--	12
128	--	2	13	--	--	--	--	15
130	--	--	14	--	--	--	--	14
132	--	2	6	--	--	--	--	8
134	--	1	10	--	--	--	--	11
136	--	1	4	--	--	--	--	5
138	--	2	7	--	--	--	--	9
140	--	2	4	--	--	--	--	6
142	--	2	11	1	--	--	--	14
144	--	1	16	--	--	--	--	17
146	--	3	15	--	--	--	--	18
148	--	2	11	--	--	--	--	13
150	--	2	8	1	--	--	--	11
152	--	2	18	--	--	--	--	20
154	--	7	13	--	--	--	--	20
156	--	8	25	1	--	--	--	34
158	--	6	15	1	--	--	--	22
160	--	7	24	1	--	--	--	32
162	--	5	23	1	--	--	--	29
164	--	1	17	1	--	--	--	19
166	--	3	19	2	--	--	--	24
168	--	4	10	2	--	--	--	16
170	--	--	23	4	--	--	--	27
172	--	1	15	1	--	--	--	17
174	--	1	25	1	--	--	--	27
176	--	1	16	6	--	--	--	23
178	--	1	11	11	--	--	--	23
180	--	--	9	6	1	--	--	16
182	--	--	4	8	--	--	--	12
184	--	1	4	8	1	--	--	14
186	--	--	2	12	--	--	--	14
188	--	--	4	8	1	--	--	13
190	--	--	2	8	2	--	--	12
192	--	--	2	6	4	--	--	12
194	--	--	1	14	2	1	--	18
196	--	--	2	5	1	1	--	9
198	--	--	--	11	8	1	--	20
200	--	--	--	3	3	--	--	6
202	--	--	--	1	2	--	--	3
204	--	--	--	4	4	1	--	9
206	--	--	1	1	6	1	1	10
208	--	--	--	--	7	--	--	7
210	--	--	--	1	3	1	--	5
212	--	--	--	--	--	1	--	1
214	--	--	--	--	2	--	1	3
216	--	--	--	--	--	--	--	--
218	--	--	--	--	1	1	--	2
220	--	--	--	--	--	1	--	1
222	--	--	--	--	--	--	--	--
224	--	--	--	--	--	1	--	1
226	--	--	--	--	--	--	--	--
228	--	--	--	--	--	--	--	--
230	--	--	--	--	--	--	--	--
232	--	--	--	--	--	--	1	1
Totals	--	69	436	130	48	10	3	696
Mean lengths	--	154	156	186	201	208	--	166

TABLE 6

Age and Year-class Composition of the Sardine Catch in the 1958-59 Season

	Catch		Number of fish in thousands by age and year-class									
			0	1	2	3	4	5	6	7	8	9
	Tons	Number	1958	1957	1956	1955	1954	1953	1952	1951	1950	1949
Central California												
"August"	4,599	52,711	--	7,095	37,789	7,664	121	--	42	--	--	--
"September"	9,174	101,471	--	11,771	70,137	18,914	568	81	--	--	--	--
"October"	5,450	58,739	--	8,141	36,248	14,268	82	--	--	--	--	--
"November"	2,917	30,992	--	1,240	25,413	4,339	--	-	--	--	-	--
"December"	2,460	27,842	-	1,114	23,610	3,118	--	--	--	-	--	--
"January"	14	159		6	135	18	--	-	--	-	--	-
Total Central California	24,614	271,914		29,367	193,332	48,321	771	81	42	--	--	--
Percent	--	100.0	--	10.8	71.1	17.8	.3	--	--	--	--	--
Southern California												
"September"	25,677	218,655		30,021	111,820	43,731	17,055	10,211	5,095	722	--	-
"October"	29,972	284,435	--	18,204	161,957	85,700	13,653	3,214	939	569	--	199
"November"	16,470	169,792	--	22,497	116,206	27,387	1,902	1,596	204	--	--	--
"December"	5,731	60,756	--	2,710	38,136	18,974	936	-	-	--	--	--
"January"[1]	157	1,558	--	69	978	487	24	--	--	--	--	--
Total Southern California	78,007	735,196	--	73,501	429,097	176,279	33,570	15,021	6,238	1,291	--	199
Percent	--	100.0	--	10.0	58.4	24.0	4.6	2.0	.8	.2	--	--
Total California	102,621	1,007,110	--	102,868	622,429	224,600	34,341	15,102	6,280	1,291	--	199
Percent	--	100.0	--	10.2	61.9	22.3	3.4	1.5	.6	.1	--	--
Baja California[2]												
"September"	653	9,490	--	1,148	7,738	589	--	15	--	--	--	--
"October"	2,213	28,327	--	2,588	19,376	4,925	1,258	180	--	--	--	--
"November"	2,955	37,080	--	4,694	28,272	4,114	--	--	--	--	--	--
"December"	1,821	34,463	--	4,561	28,261	1,641	--	--	--	--	--	--
"January"[1]	151	2,535	--	--	2,281	254	--	--	--	--	--	--
Total Baja California	7,793	111,895	--	12,991	85,928	11,523	1,258	195	--	--	--	--
Percent	--	100.0	--	11.6	76.8	10.3	1.1	0.2	--	--	--	--
TOTAL	110,414	1,119,005	--	115,859	708,357	236,123	35,599	15,297	6,280	1,291	--	199
Percent	--	100.0	--	10.4	63.3	21.1	3.2	1.4	.5	.1	--	--

[1] December 24 to January 1 only.

Details of the method are given by Felin and Phillips (1948, p. 11). Necessary to the method are weight-per-fish factors. This season's averages of these factors were: central California 0.1784 pounds; southern California 0.2091 pounds; and Baja California 0.1212 pounds. The age and year-class compositions of the catches of central and southern California and Baja California (for the corresponding California season) are presented in Table 6.

The 1956 class was the most abundant in the fishery in all regions. It contributed almost two-thirds of the total number of sardines landed during the season. The 1955 class, which contributed almost one-quarter of the southern California catch, was second in the total landings, contributing over one-fifth. About one-tenth of the total were fish of the 1957 class. Fish older than the 1955 class made up only one-twentieth of the total catch.

During the Baja California interseason the 1956 class made up almost three-quarters of the total catch (Table 7).

TABLE 7

Year-class Composition of the 1958 Interseason Sardine Catch for Baja California [1]

Lunar month	Catch		Number of fish in thousands by year-class						
	Tons	Number	1958	1957	1956	1955	1954	1953	1952
"Jan" [2]	1,851	44,911	--	--	36,557	1,078	3,054	2,695	1,527
"Feb"	715	17,335	--	--	14,111	416	1,179	1,040	589
"Mar"	869	20,478	--	914	16,278	1,854	1,210	173	49
"Apr"	1,160	14,196	--	241	2,917	8,632	2,045	361	--
"May"	920	11,548	--	490	4,279	5,052	1,289	309	129
"Jun"	832	13,097	--	2,822	9,880	291	104	--	--
"Jul"	2,360	35,408	--	5,004	29,213	1,096	95	--	--
"Aug"	2,883	35,880	--	4,160	28,808	2,912	--	--	--
Total	11,590	192,853	--	13,631	142,043	21,331	8,976	4,578	2,294
Percent	--	100.0	--	7.1	73.6	11.1	4.6	2.4	1.2

[1] Tonnage figures from Ensenada and Cedros Island; sampling of commercial catch for age composition at Ensenada only.

[2] No fish were sampled at Ensenada during "Jan". Number of fish and age composition derived from "Feb" sampling.

DISCUSSION

The most interesting feature of the 1958-59 season was the dominant role of the 1956 class of sardines. This class had been primarily responsible for the resumption of the central California fishery after a seven-year lull, and for making this season's total catch from all regions the largest in those seven years. This dominance is surprising in that there was little advance notice of it. During the 1957-58 season in southern California the 1956 class did not contribute an unusual proportion of age-one fish to the commercial catch (Daugherty and Wolf, *op. cit.*, Table 4). Only in the relatively minor Baja California fishery, and then only in "December", did it show evidence of being of more than usual abundance.

The 1956 class fish have been smaller than average. They were relatively small as age-one fish in Baja California during the 1957-58 season (Daugherty and Wolf, *op. cit.*, Table 2). During the 1958-59 season they were still relatively small as age-two fish. In central California mean lengths of age-two fish during 19 earlier seasons ranged between 195 and 213 mm. and averaged 204 mm. This average is 20 mm. greater than the mean of 184 mm. observed in this region during the 1958-59 season. In southern California the range of mean lengths was 194 to 224 mm. over 24 seasons with an average of 204 mm. This average is 13 mm. larger than the 1958-59 seasonal mean of 191 mm. The Baja California means ranged from 193 to 207 mm. and averaged 200 mm. for four seasons. This was 40 mm. greater than the 160 mm. mean observed during the 1958-59 season. In all regions this season's mean for age-two fish was not only lower than the long-time average, but was also the lowest mean length so far observed.

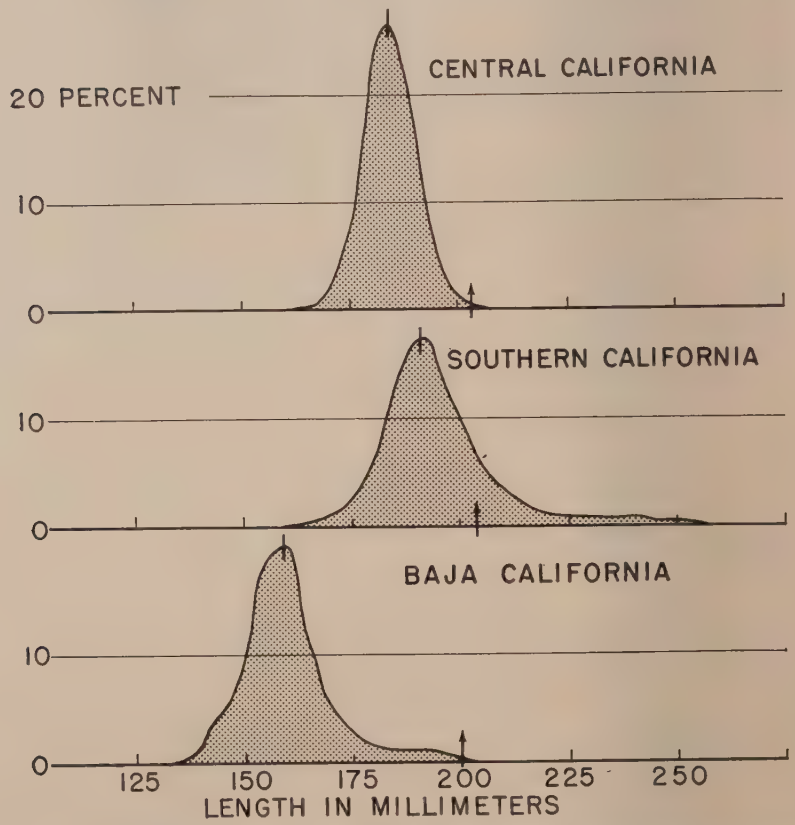

FIGURE 3. Percentage length composition of the sardine catch by region during the 1958-59 commercial season. Marks near modes are average length of age-two fish during this season. Arrows on length scale lines locate average length of age-two fish over earlier seasons.

In Figure 3 the length composition of the total catch in each region is shown. The peaks of the curves represent 1956 class fish almost entirely, however. Marked on the curves are the mean lengths of 1956 class fish in each region for the season. On the length scale line, the long-term means of age-two fish have been entered. The figure illustrates the differences between means within a region, and in addition shows that fish of the same year-class also vary considerably in length between regions.

SUMMARY

1. The 1958-59 season began on August 1 and ended on January 1 in central California and on September 1 and January 1 in southern California. Sardine fishing in Baja California occurred throughout the year but, for purposes of this paper, the time was divided into two periods, one comparable to the southern California season and the other an interseason period.

2. The California commercial catch of Pacific sardines during the 1958-59 season was 102,621 tons of which over 24,600 tons were from central California and over 78,000 tons from southern California. During the same season in Baja California almost 7,800 tons were taken. This added to an interseason total of almost 11,600 tons made the Baja California landings total approximately 19,400 tons during 1958.

3. California fishermen received $60 per ton for their fish through "September"; thereafter they received $50 to the end of the season. Baja California fishermen received the equivalent of $40 per ton all year.

4. Around 180 boats were involved in the season's sardine fishery: 30 from central California, 119 from southern California, and about 30 from Baja California.

5. Length composition data, by age, based on samples from the commercial catch are presented for central California, southern California and Baja California.

6. Age composition estimates for the entire season's catch are presented for central and southern California and Baja California. Age composition data from the Baja California interseason's catch are also given.

7. The dominance in this season's catch of the 1956 class of sardines in all regions is pointed out and briefly discussed.

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YEARLY CHANGES IN THE PERU CURRENT

BY WARREN S. WOOSTER

Yearly Changes in the Peru Current[1]

The scientific investigation of the Peru Current in the past has been a sporadic effort, punctuated by the occasional visit of a British, American or other foreign research vessel, followed in a decade or two by a flurry of scientific reports. The systematic observation of changes in the current system, so essential to an eventual understanding of its normal and abnormal functioning, has been almost nonexistent. Fortunately, nearly 20 years ago, Dr. Erwin Schweigger of the Peruvian Compañia Administradora del Guano had the foresight to initiate the collection and compilation of sea-surface temperature and weather observations from Peruvian vessels, so that there exists, sparse though it may be, a record of ocean changes since the year 1939.

The accumulated data have been published (in the recently discontinued *Mapas Mensuales* of the Guano Administration) by half-degree squares, in most of which too few data are available to permit the calculation of meaningful averages. However, along the coastal shipping routes it is possible to select for each parallel of latitude a one-degree square containing the maximum number of observations (Fig. 1). I have calculated mean surface temperatures for these squares for each month of each year for the period 1939 through 1956. As shown by the inset, the annual range of temperature varies from about 4°C at 12°S to nearly 6°C at 4°S.

The grand averages of these data are shown in an isogram (Fig. 2) which illustrates the seasonal change of surface temperature along the Peruvian coast. Highest temperatures, up to more than 22°C, are found farthest north (*i.e.*, nearest to the

[1] Contribution from the Scripps Institution of Oceanography. Paper delivered at meeting of Pacific Section, American Society of Limnology and Oceanography, San Diego, 17 June 1959. The work was supported in part by the Peruvian Consejo de Investigaciones Hidrobiológicas, and by the Office of Naval Research and the Bureau of Commercial Fisheries through contracts with the University of California.

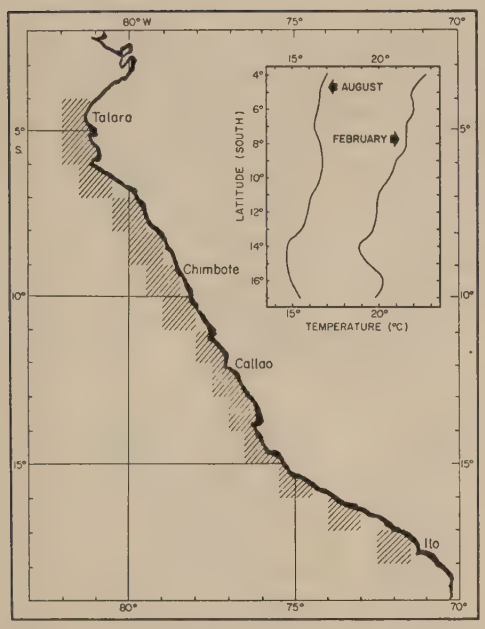

FIG. 1. One-degree squares used in analysis. Inset shows average February and August surface temperatures for period 1939–1956.

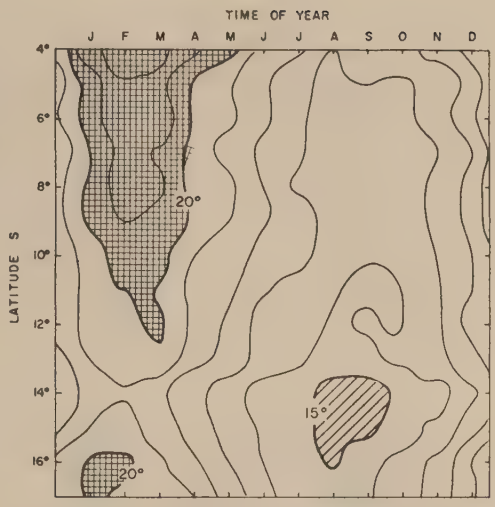

FIG. 2. Average surface temperature for one-degree squares for period 1939–1956, from Wooster (1960).

equator) in the summer, February and March being the months in which warm waters extend farthest south. The summer warming in southernmost Peru is separated from that in the north by colder water at 14° and 15°S. Indeed, during all months of the year lowest temperatures are found at those latitudes. Only there do average temperatures fall below 15°C during the winter cool period, which seems to be best developed in August, September and October. The most conspicuous event of the year appears to be the oncoming of summer, with temperature changes of several degrees per month, whereas during the rest of the year the average rate of change is one degree per month or less.

The detailed yearly isograms (Figs. 3 and 4), as one would expect, are much more irregular in appearance, primarily because of the much smaller number of observations involved (when less than 6 observations were available for a given square, the average was not used). The alternation of seasons is still plainly visible. Obviously not all years are the same, and the differences between years are often striking.

For example, waters warmer than 20°C were first observed off northern Peru as early as November, 1940, two months before usual, and by January, 1941, the warm region extended southward to at least 16°S, with temperatures from 2°C to nearly 5°C higher than normal. In February and March temperatures in excess of 25°C were observed north of 9°S, and the presence of water several degrees warmer than usual persisted through June. Disappearance of the warm regime was abrupt, with surface temperatures dropping 2–3°C in a month to the north of 12°S.

This "El Niño" of 1941 has been described by several investigators (Schweigger 1942; Sears 1954; Lobell 1942; Vogt 1942). Its principal characteristic, as shown by these temperature charts, is the marked increase in southward penetration, duration and intensity of the annual summer warming off the Peruvian coast. Another year, 1953 (Fig. 4), which has been considered a Niño year (Posner 1957), shows some of the same features, although to a smaller extent.

Other years are clearly colder than usual, the period 1950–51 presenting an interest-

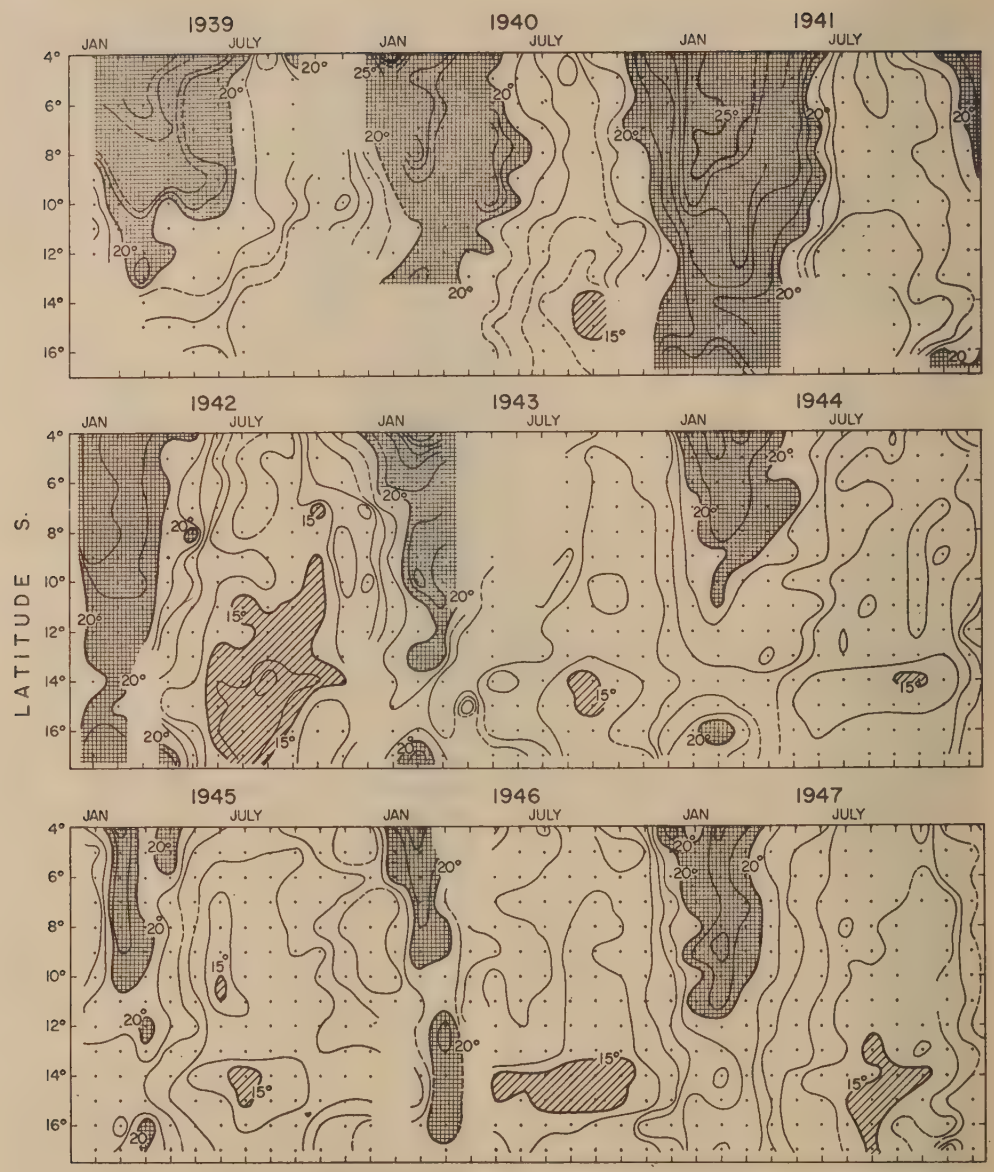

FIG. 3. Average surface temperature for one-degree squares, for individual years 1939 to 1947.

ing example. The summer warming of 1950 was notably reduced; even in northern Peru, surface temperatures remained below 20°C, from 2° to 3.5°C cooler than usual. The winter cold regime was well developed, and the warming of early 1951 was again weak. Then conditions changed rapidly in May, 1951, with a wintertime development of waters warmer than 20°C extending as far south as 13°S, a feature apparent nowhere else in the available record.

Although it is obviously impossible to account for all the features of these records,

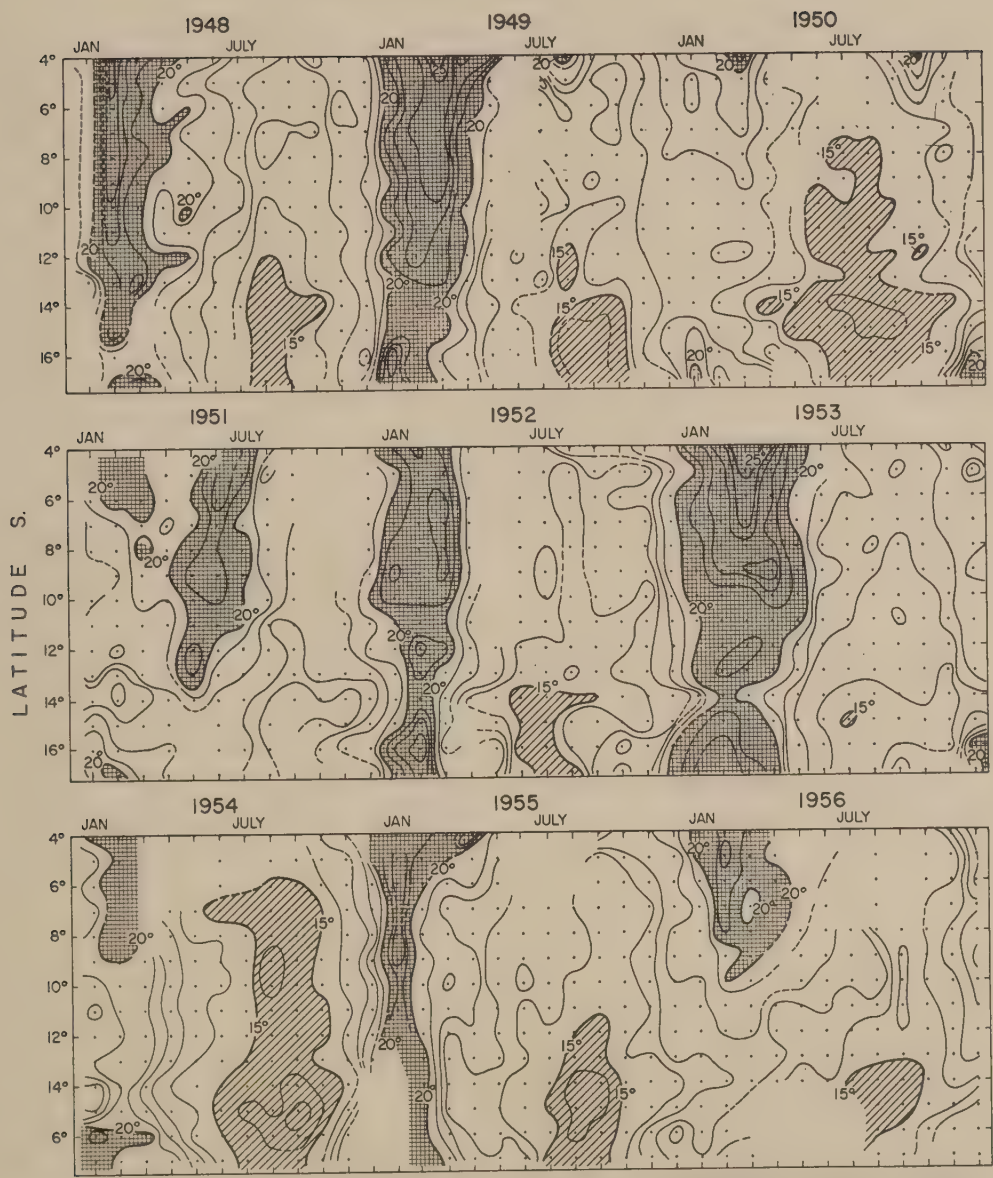

FIG. 4. Average surface temperature for one-degree squares, for individual years 1948 to 1956.

the general trends are not so inexplicable. During the winter the strongly developed southeast trades are responsible for the optimal development of upwelling, so that low temperatures prevail along the entire coast. The zone of lowest temperatures, at 14° to 15°S, is located where there occurs a 30° change in direction of the coast line relative to that of the average wind. During the summer the intertropical convergence is at its southernmost latitude, as is the north boundary of the Peru Current, and the weakened southeast trades are less effective in producing upwelling.

If this picture of seasonal change in the Peru Current region is essentially correct,

it seems reasonable to expect that the major non-seasonal changes are linked to major variations in the surface wind circulation. The events of 1941 could be interpreted as indicating an abnormal weakening of the trade wind circulation (Wooster 1960). The low temperatures of 1950–51 could result from stronger than usual southerly winds along the Peruvian coast. The recent work of Bjerknes (1959), Roden and Groves (1960), Roden and Reid (in press) and others tends to support such an interpretation, although temperature-wind correlations do not yet give as clear-cut an answer as one might wish. Unfortunately in the southern hemisphere the supply of reliable historical weather data seems to be small. If usable data can be located, it seems likely that the picture of yearly change suggested by these surface temperature isograms will be relatively simple to explain.

FOOTNOTE

Since completion of this work, Schweigger (1959; Fig. 6 A, 6 B) has published surface temperature isograms for the period 1948–1956 based on a somewhat different interpretation of the same data.

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LETTER TO THE EDITORS

Further evidence of a Pacific south equatorial countercurrent

(*Received* 8 *June* 1961)

REID (1959) has presented evidence of a south equatorial countercurrent in the Pacific Ocean, flowing eastward along a surface of constant thermosteric anomaly 125 cl/T ($\sigma_t = 26{\cdot}81$) at speeds of 10 to 25 cm/sec. The latitude of this flow changes from 2°–5°S at 165°E to 10°–14°S at 95°W. The depth of this surface is approximately 300–400 m, but there is also some evidence of a surface current at least between 170°E and 135°W and possibly as far east as 95°W. The evidence is based on a geostrophic analysis of oceanographic station data, but in the western Pacific there are also some indications of the flow in atlases of surface currents prepared from observations of ship set and drift.

A recent chart of surface geostrophic flow relative to the 1000 decibar surface (REID, ms) clearly shows the eastward surface flow, which appears to be stronger in the west than in the east. However, the scarcity of suitably located oceanographic stations in the eastern south Pacific leaves somewhat uncertain the nature of the current in that region. Therefore a detailed profile of observations extending along the meridian 95°W (from 23° 40′S to 10°N) was included in the programme of the University of California's STEP–I Expedition. This profile was made during the period 25 November to 7 December 1960, approximately the season for which REID predicts the farthest eastward extension of the south equatorial counter current.

Examination of a profile of geostrophic speed* perpendicular to the section (relative to the 1000 decibar surface) shows eastward flow of 4 to 9 cm/sec at the surface between 5° and 8°S (FIG. 1), the difference in level across the flow being 4 dyn. cm. Stronger flow, up to 10 cm/sec, is apparent at depths of 100 m to 200 m, and the subsurface currents appears to extend somewhat farther north (to 4°S). Eastward transport of this current is estimated as 12×10^6 m^3/sec.

Although eastward flow is evident on the thermosteric anomaly surface 125 cl/T, principal motion appears at shoaler depths, the isanostere of 160 cl/T lying close to the highest subsurface speeds. On that isanosteric surface the water has slightly higher salinity than do the waters to the north or south (34·92–34·93 ‰ as opposed to 34·90 ‰ or less†). This is consistent with REID's (1959) statement that in the western Pacific the path of eastward flow coincides with a tongue of high salinity extending eastward from a maximum value in the Coral Sea.

Strong eastward flow is also apparent (FIG. 1) between 2° and 3°S, but this circulation appears to be a separate phenomenon and is probably part of the system peculiar to the immediate vicinity of the equator.

In the equatorial Pacific the meridional slope of the thermocline is a reliable indicator of the location and relative intensity of the near-surface zonal currents. A bathythermograph section across the south equatorial countercurrent shows the thermocline sloping slightly downward towards the equator (FIG. 2), consistent with geostrophic flow to the east. Comparison of a station at the southern edge of the current (Sta. 75) with one in its centre (Sta. 77) indicates that the slope of the isotherms extends to considerable depths, the layer between 150 m and 600 m being significantly warmer on Sta. 77 (as much as 0·9° at 300 m). This higher temperature is primarily responsible for the higher thermosteric anomaly on Sta. 77, the values being 5 to 10 cl/T higher throughout the indicated layer. In this layer the waters on Sta. 77, in the current, have slightly more dissolved oxygen (0·2 to 0·5 ml/l more) and silicate (about 5 μg at/l more) and slightly less phosphate (0·1 to 0·25 μg at/l) than on Sta. 75.

*In making the hydrostatic computations, the pressure terms of specific volume anomaly were neglected (that is, thermosteric anomaly was used rather than specific volume anomaly), the approximation being considered adequate for the purposes of this paper (MONTGOMERY and WOOSTER, 1954).

†Salinity measurements were made with a conductivity-type salinometer, the precision of which appears to be better than ± 0·01‰ in salinity units (PAQUETTE, 1959).

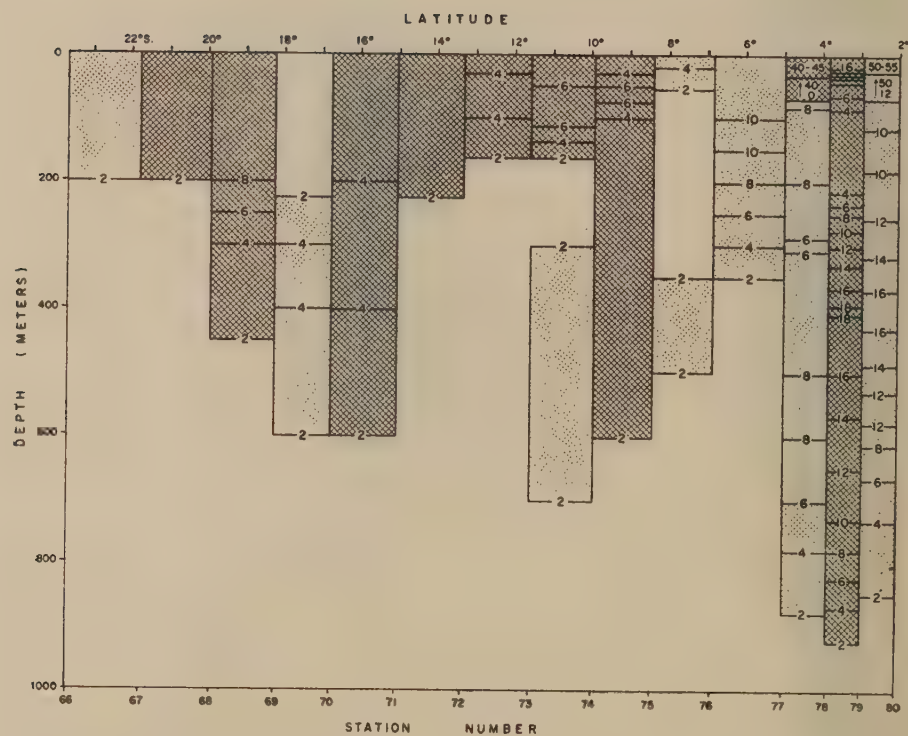

Fig. 1. Geostrophic speed (cm/sec, relative to the 1000 decibar surface) perpendicular to profile at 95°W. Light shading represents flow to the east, dark shading to the west.

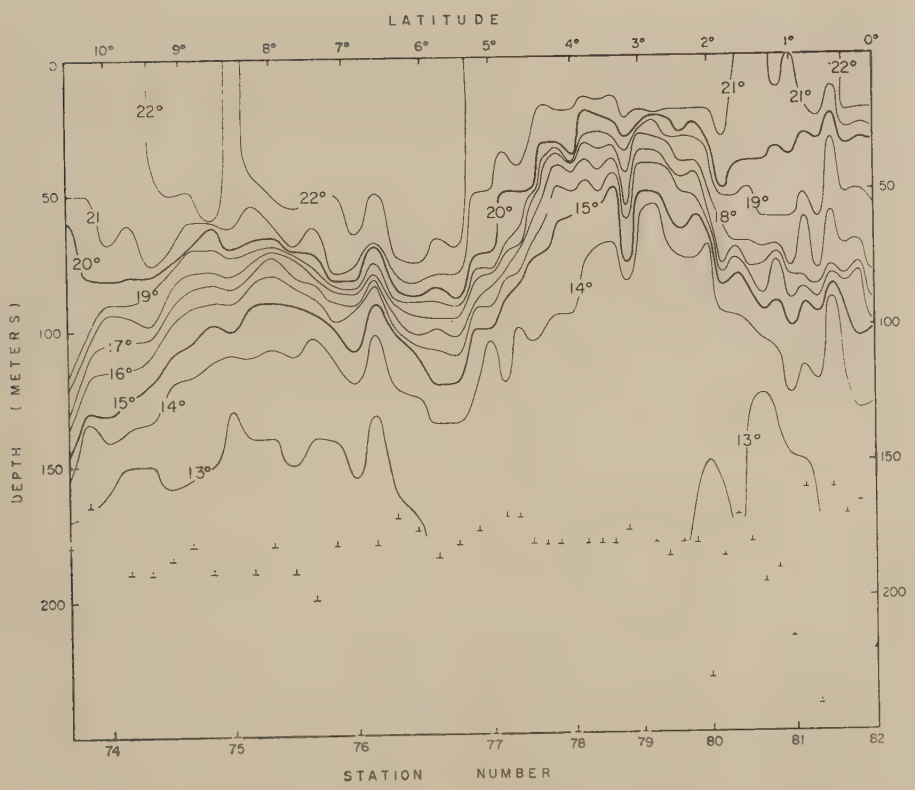

Fig. 2. Vertical temperature distribution along portion of profile at 95°W, as measured by bathythermograph.

Because of these rather subtle differences in the physical and chemical properties of the waters of the south equatorial countercurrent, it would be interesting to examine plankton collections for species which might serve to identify the current.

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Bow Wave Riding of Dolphins

Abstract. Dolphins riding bow waves were observed through underwater viewing ports. The postures assumed by the dolphins show that they present their bodies rather than the ventral surfaces of their flukes to the propellant forces of the bow wave.

How dolphins ride bow waves is the subject of a current controversy. After observing them performing this feat through underwater viewing ports in a ship's bow, I would like to report the method the dolphins themselves seem to consider proper.

Since Woodcock (*1*) noticed the "motionless" swimming of dolphins and interpreted it as bow wave riding, several proposals attempting to reconcile it with hydrodynamic theory have been advanced. Woodcock and McBride (*2*) concluded that only under conditions of laminar flow and nonbuoyancy could a dolphin sufficiently overcome drag to get a ride. Hayes (*3*) then showed in a terse presentation of calculations of hydrodynamic forces that the buoyancy of a dolphin in a pressure gradient determined the amount of hydrodynamic lift needed but did not affect the drag. Approaching the problem experimentally, Scholander (*4*) concluded that the tail flukes of a dolphin in the incline of a bow wave and properly angled up into the incline would be subject to enough force to push the whole animal forward. Objections by Hayes (*5*) to Scholander's hypothesis and a rebuttal by Scholander (*6*) were printed in *Science*. A point in disagreement was whether the forward component of the bow wave forces acted on the entire dolphin or just on its flukes. Fejer and Backus (*7*), stating that Hayes's explanation was correct but incomplete, supplied more observations on porpoises and computations on the nature of the pressure field and the function of ship's length and drag coefficient on the position of a wave-riding porpoise.

Underwater observation ports installed in the bow of the *Charles H. Gilbert* (Fig. 1)—research ship of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii—in early 1960 for the purpose of studying tuna behavior provided excellent facilities for observing and photographing dolphins riding the bow wave. Since that time I have had occasion to observe several species of dolphins off the coast of northern California, off the coast of Mexico, and near Kingman Reef in the central equatorial Pacific. Motion pictures were successfully taken at the last location.

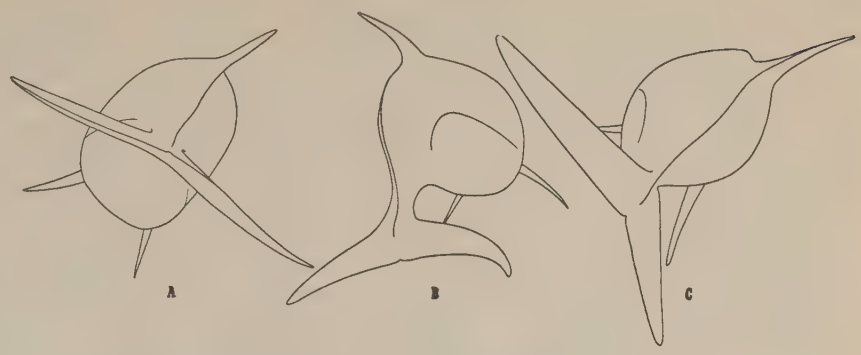

Fig. 2. Postures of *Tursiops* sp. while riding a bow wave.

Porpoises did not always find the bow wave suitable for riding. When they first approached, they swam from side to side in front of the ship for a few minutes, apparently testing the pressure field, before they engaged in wave riding or left.

The field observations and reviews of the movie show that the dolphins assume several attitudes. The range of postures they assumed while riding the bow wave of the ship, which traveled at about 9 knots is shown in the outline drawings taken directly from the film (Fig. 2). The posture shown in Fig. *2B* is the one most commonly seen. The trailing edge of the flukes was an estimated ½ to 3 feet ahead of bow. The position and predominant posture of the dolphins indicate that their bodies are used to take advantage of the forward component of the forces of the bow wave. Moreover, they were never seen riding with their flukes angled in conformance with Scholander's hypothesis. The flukes seemed to be used solely to control hydrodynamic lift.

Although the dolphins often rode steadily, without changing their positions relative to the bow wave, they seem to prefer weaving laterally in and out among each other. In doing so they continually changed their vertical positions by as much as 3 feet and thus exhibited excellent control of hydrodynamic lift and stability by changing the planes of their pectorals and flukes,

Fig. 1. Underwater viewing ports in the bow of the *Charles H. Gilbert*.

bending their bodies, and banking. Implied in Hayes's explanation is the necessity of lift control to enable the dolphins to meet exigencies caused by buoyancy changes. Therefore, although such control was postulated (*6, 8*) to support Scholander's hypothesis, this assumption also supports Hayes's explanation (*9*).

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9. I wish to thank R. A. Barkley for clarifying some points in hydrodynamics. This report is published by permission of the director, U.S. Bureau of Commercial Fisheries.

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Plankton Pigments in East Lagoon, Galveston, Texas

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ABSTRACT

Pigment analyses have been made of a lagoon emptying into the Gulf of Mexico. This water showed a typical cycle of early spring flowering, later spring minimum, summer oscillations, and a secondary early fall maximum. The cycle resembled those of more northern waters, but the blooms in East Lagoon occurred earlier in the year. The bloom periods were related to various physical factors—solar radiation, temperature, and rainfall—with a direct relationship between incident radiation and chlorophyll *a* production indicated for the fall of 1957. The chlorophyll production of the lagoon compared favorably with other waters in these latitudes, yielding a mean of 17.6 mg chlorophyll a/m^3 during the sampling period from October 1957 to May 1959. An analysis of the precision of the method indicated a standard error of 0.565 ± 0.085 mg/m^3 for chlorophyll *a* and 1.35 ± 0.165 MSPU/m^3 for chlorophyll *c*. The large value for the latter pigment is attributed to the method of calculation.

INTRODUCTION

The analysis and measurement of plankton pigments is now a standard practice in the fields of limnology and oceanography. Dating from the time of Willstatter and Stoll who related plant pigments (more particularly chlorophyll *a*) to the amount of photosynthesis, various authors have used this measurement either to indicate standing crop or as an index of the potential production of an area (Ryther, 1956). In the present report pigments have been used as an index of standing crop in a sub-tropical estuary in conjunction with a study of the effects of a copper ore dike upon the ecology of East Lagoon, Galveston, Texas. Data were gathered for 11 months prior to the addition of copper ore in the lagoon and for the following 9 months. Since no marked effects due to the ore itself were noted (Marvin, 1959), only the effects of the yearly climatic cycle upon the standing crop and potential production will be discussed.

METHODS

The lagoon is a narrow body of water 1.1 miles long and 230 feet wide at the narrowest point with a volume of approximately 75 million gallons. Figure 1 shows the location of the lagoon and the sampling stations with reference to the Houston Ship Channel. The Gulf of Mexico is approximately one-fourth mile south of the lagoon at its closest point. Stations were numbered from the head of the lagoon, with station 1 being the deepest (4.4 meters) and receiving the greatest amount of drainage from the surrounding marsh. Stations 7 and 8 at the mouth of the lagoon were 2.5 meters deep and were subject to greater tidal action than the others. The ore dike, when established, was placed between stations 3 and 4 which were intermediate in depth. All stations were along the deeper axis of the lagoon.

The frequency of sampling varied during the experimental period. With few exceptions, samples were taken at least twice each week from the inception of the work in October 1957 until the end of October 1958, after which weekly samples were taken. Eight stations were sampled until December 1958 when the stations sampled were reduced to stations 1, 4, and 7. Samples were taken at the same time of day to minimize differences due to light intensity.

Fifty gallons of water were pumped into a polyethylene drum at each station while the intake hose was moved up and down from the surface to within a foot of the bottom. The temperature of this composite sample was taken, and 2-liter samples were then removed for analysis. Salinities were taken with a hydrometer and the samples treated with $MgCO_3$ immediately upon return to the laboratory. After overnight storage in a refrigerator, the samples were stirred and 1 liter filtered through a Millipore apparatus (Creitz and Richards, 1955) and the residue extracted with 90 percent reagent-grade acetone (Richands with Thompson, 1952) for the determination of plankton pigments. The extraction was

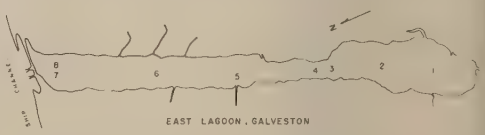

FIGURE 1.—East Lagoon, Galveston, Texas, showing stations sampled.

TABLE 1.—*Precision of the method*

Pigment	Number of samples	Mean pair difference (MSPU or mg/1 of extract)	Standard error of mean
Chlorophyll *a*	141	0.113	±0.017
Chlorophyll *b*	141	0.060	±0.008
Chlorophyll *c*	141	0.270	±0.033
Astacin-type carotenoids	141	0.030	±0.003
Non-astacin carotenoids	141	0.072	±0.006

allowed to proceed in the dark for 18 to 24 hours at room temperature after which the optical densities of the extracts were read in a Beckman DU spectrophotometer at 665, 645, 630, 510, and 480 mμ and the amount of pigment calculated.

PRECISION OF METHOD

For the first 2 months of the project each 2-liter sample was divided in half and each liter filtered, extracted, and read as a separate determination. Table 1 shows the precision based upon 141 of these duplicate samples. The chlorophyll *c* values showed greater pair differences than those of any other pigment. This may in part be ascribed to the method of calculation, for instrumental readings are multiplied by a factor of 100. Thus a slight instrumental or operator error may have resulted in larger variations in the final calculated value for chlorophyll *c*. Greater pair differences in chlorophyll *a* tend to occur when larger quantities of pigment are present. This may be due in part to errors in extraction, as cited by Odum, McConnell, and Abbott (1958), when plankton blooms are occurring. Extraction errors may result from the presence of heavy walled organisms which are difficult to break up with the usual trituration and extraction so that duplicate samples may not be extracted equally well. There may also be a constant percentage error inherent in the procedure, resulting in larger differences at higher pigment concentrations.

A second type of precision study was also carried out. Fifty gallons of water were pumped from a single station, and from this amount eight 2-liter samples were returned to the laboratory for analysis. Duplicates of each sample were analyzed as described in the preceding section. These analyses indicated that the values reported for the duplicates were more precise than the values for replicates from one sample. For this reason, only single samples were taken during the latter phase of the project.

TABLE 2.—*Destruction of pigments by heat and light*

Pigment	Original concentration (mean)	Final concentration (mean)	Percentage of original
Chlorophyll *a*	4.55 mg/1	2.09 mg/1	45.0
Chlorophyll *b*	0.18 mg/1	0.12 mg/1	63.7
Chlorophyll *c*	2.03 MSPU/1	1.36 MSPU/1	66.9
Astacin carotenoids	0.26 MSPU/1	0.31 MSPU/1	123.1
Non-astacin carotenoids	1.33 MSPU/1	0.65 MSPU/1	46.0

A further check was made on the stability of the pigments in samples untreated with $MgCO_3$ and not refrigerated. The $MgCO_3$ served to prevent the breakdown of the chlorophylls to the corresponding pheophytins whose absorption peaks do not correspond to the peaks of the original compounds. Refrigeration inhibited bacterial action, as well as the action of light and heat in the destruction of the pigments. A single set of eight samples (duplicates of a set previously treated and analyzed) was held without the addition of $MgCO_3$ at room temperature for 3 days following collection. At the end of this time they were treated, extracted, and read as usual. The change in each type of pigment under these conditions emphasized the need for prompt treatment and analysis (Table 2). It further indicated the necessity for analysts, in reporting on work of this kind, to state the type of treatment given to the sample and the length of time it was held prior to analysis.

Table 2 shows that about 55 percent of both the chlorophyll *a* and the non-astacin carotenoids were destroyed by room light and temperature. Chlorophyll *b* and *c*, on the other hand, have suffered only about 35 percent destruction, and the astacin-type carotenoids have apparently increased. Some of these differences are undoubtedly due to the spectral shifts, mentioned above, when a pigment is converted to a degradation product. However, it is noteworthy that the chlorophyll *c* values remained relatively high so that the chlorophyll *a* to chlorophyll *c* ratio, which has been used by some authors to characterize inshore and offshore waters (Currie, 1958), decreased by about one-third.

RESULTS OF SURVEY

As stated earlier, the regular sampling of the lagoon for plankton pigments began in October 1957 and continued until the end of May 1959. Figures 2 through 7 show the cycle in the lagoon of chlorophyll *a* (mg/m^3), chlorophyll *c* (MSPU/m^3), non-astacin or plant-type carotenoids (MSPU/m^3), solar ra-

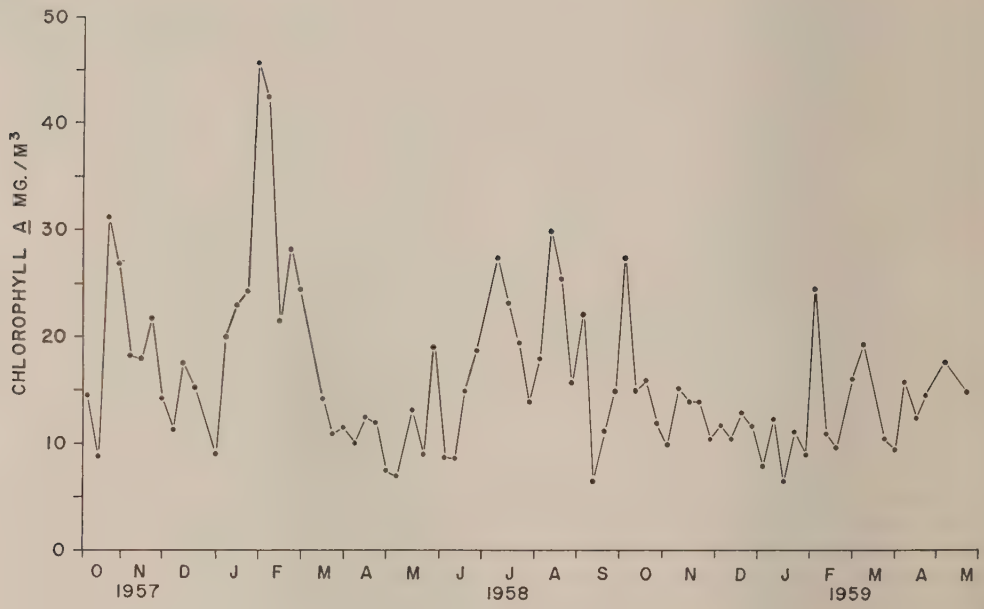

FIGURE 2.—Variation in weekly means of chlorophyll *a* measurements

diation, air temperature, salinity, and rainfall. The values for all data are expressed as the daily mean of all stations for a weekly period (other than rainfall which is expressed as total rainfall per week). The solar radiation data were calculated by the method of Fritz and MacDonald (1949) using the data of the Galveston Weather Bureau for percentage of possible sunshine per day. The air temperatures are means of the daily Weather Bureau observations. Salinity and pigment quantities are means only of the days and times at which samples were taken.

Figure 2 presents mean daily cholorphyll *a* concentrations for the eight stations for the entire period of sampling. An early fall maximum occurred in October in both 1957 and 1958, with a maximum mean of 31.2 mg/m^3 in 1957 and 26.8 mg/m^3 in 1958. The spring phytoplankton flowering began early in January of 1958, and reached its peak during the last week of the month when the mean chlorophyll *a* concentration reached the maximum of 45.8 mg/m^3. The highest value recorded during the bloom was 61.1 mg chlorophyll *a*/m^3 at station 1, but values of 50 mg/m^3, or more, were recorded at all stations. The bloom gradually decreased to a spring and early summer minimum in the months of March through June, followed by a gradual increase with periods of oscillation during July and August. This latter period was characterized by patchy euglenoid blooms throughout the lagoon area, and during one of these the highest value of the survey, 84.5 mg/m^3, was recorded at station 1. This was followed by a more general bloom throughout the lagoon, with a mean of 29.8 mg/m^3, but values were never again as high as those recorded during the spring of 1958. Conditions during September 1958 were disturbed by hurricane Ella which flooded the entire lagoon area introducing large amounts of salt and fresh water. This flooding was immediately succeeded by a marked drop in chlorophyll and other pigments to the low for the observation period, but the depression was only temporary. Immediate increase in values indicated a fall bloom which did not reach the proportions of the fall bloom of 1957. This bloom was followed by a prolonged winter period of low concentrations with a minimum in January. The spring maximum of 1959 occurred in early February, approximately 2 weeks later than in 1958, and apparently did not reach the height of the bloom the year before. These data, however, must be interpreted cautiously since there was a period of almost 3 weeks when no samples were taken, and both sampling frequency and

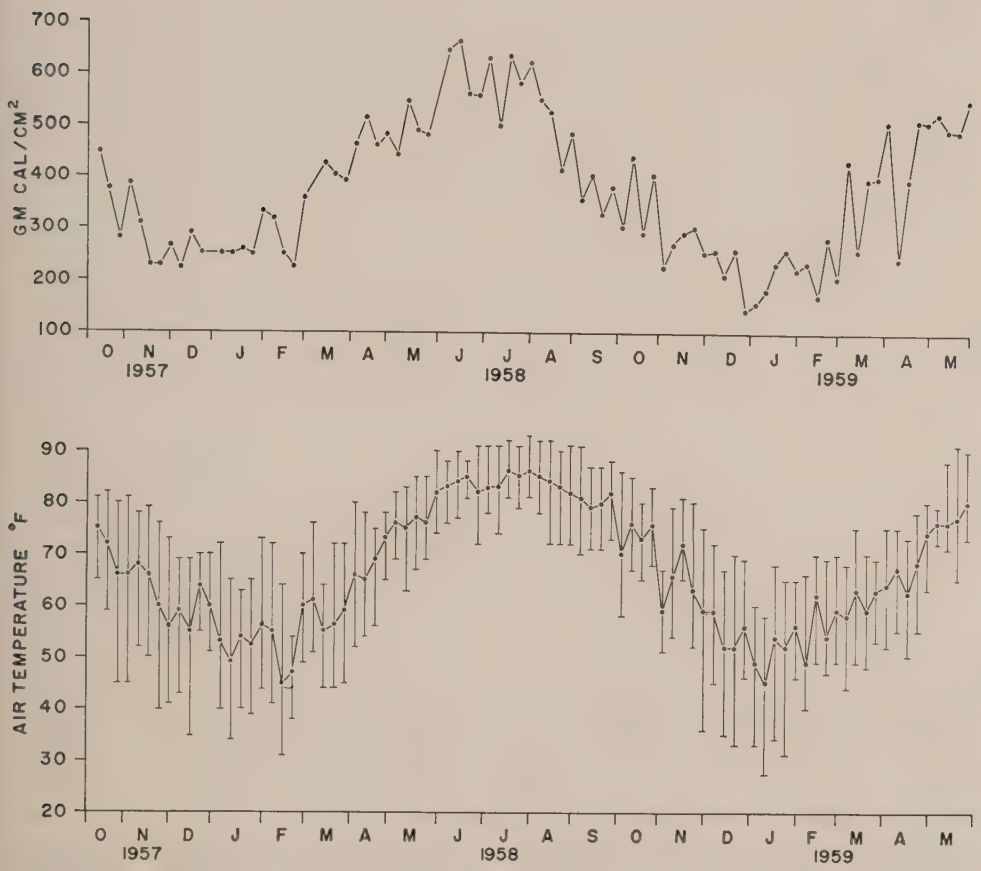

FIGURE 3.—Mean weekly solar radiation and air temperature for the Galveston area. Vertical lines on the temperature graph show the temperature range for each week.

the number of stations sampled had been reduced. The highest value recorded during this period was 26 mg chlorophyll a/m^3 from station 1. Thus, this body of water showed evidence of a cycle in phytoplankton flowering, with peaks in chlorophyll quantity in January or February and again in October–November. The minima occurred in December–January and again in April–May.

The differences in the crops of these years, as shown by the pigment analyses, may be explained in part by the accompanying physical conditions. The solar radiation graph (Figure 3) clearly indicates that there was considerably less light reaching the area during the late fall and winter of 1958 than during the corresponding period of 1957. Similarly, temperatures were lower during the winter of 1958. Since light and heat are two of the requisites for a bloom, the reduction of these may have delayed its onset in the spring of 1959.

Scatter diagrams of solar radiation versus chlorophyll present in the water indicated no relationship that held for the entire period. As has been noted in more northern waters (Smayda, 1957), the autumn and spring flowerings occurred at a time when the radiation curve was changing more or less rapidly. In East Lagoon there was a direct relationship between radiation and chlorophyll *a* for 10 weeks during 1957 (October through December) when the mean daily solar radiation was plotted against the mean daily chlorophyll of the second following week (Figure 4). The relationship would seem to indicate that at the period of declining bloom, light itself may have been the factor limiting the bloom. At

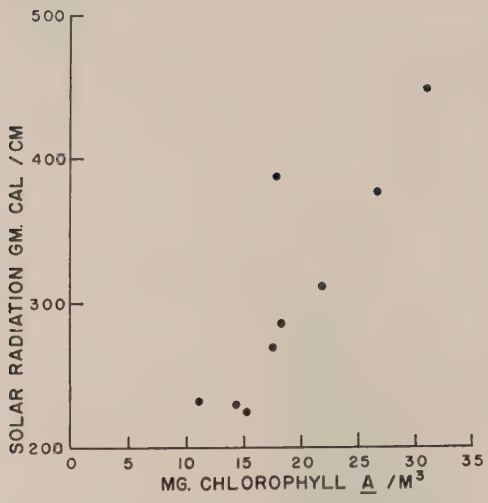

FIGURE 4.—Relation of mean solar radiation and mean chlorophyll *a*, October through December 1957.

no other period during the survey could any relationship be found. Several factors might have been responsible for the lack of correlation in the fall of 1958. They were hurricane Ella, which occurred early in September and flooded the entire area; the presence of the copper ore dike which was placed between stations 3 and 4 during August and October; and the decreased sampling frequency which might have masked the effect of light since the graphs are based on weekly means. In any case, during other periods of the survey other factors apparently had more influence on the growth of phytoplankton than solar radiation.

RELATIONSHIPS OF THE PIGMENTS TO ONE ANOTHER

Generally it may be stated that chlorophyll *c* rose and fell with the rise and fall in chlorophyll *a* (Figures 2 and 5), with the highest recorded value 34.2 MSPU/m^3 at station 1. In one bloom period chrorophyll *c* tended to drop somewhat later than chlorophyll *a*. Chlorophyll *c*, however, apparently was not destroyed as rapidly in the laboratory as chlorophyll *a* so that its later decline may have been an artifact. The ratio of chlorophyll *c* to chlorophyll *a* was greater than one in only 49 of 962 samples examined. This finding agrees with Currie (1958) who stated that ratios below one were characteristic of inshore waters, while the higher values appeared to be characteristic of offshore waters. These differences in ratio may be indicative of a change in population type, since Strain *et al.* (1943) and others have shown that diatoms and dinoflagellates are relatively rich in chlorophyll *c* whereas this pigment is absent from euglenoids and green algae.

Though fairly large quantities of chlorophyll *b* occur in terrestrial plants, only small quantities occur in many planktonic forms. During these investigations the highest recorded value was only 6.7 mg/m^3 in the fall bloom of 1958 when euglenoids were known to be present. There were only eight samples examined in which the chlorophyll *b* concentration reached 5.0 mg/m^3. Even in these samples, however, the chlorophyll *b* was found to represent less than 20 percent of the chlorophyll *a* value and less than 10 percent of the total chlorophyll present. In most cases chlorophyll *b* was found to be less than 10 percent of the chlorophyll *a* value, as might be expected in populations consisting largely of diatoms, dinoflagellates, and euglenoids (Strain, 1951). Ratios above 10 percent occurred with slightly greater frequency at station 1 than at any other station in the lagoon. This probably indicates a slightly different type of community in this area, which was also the site of the heaviest bloom found in the lagoon and the greatest single chlorophyll concentration reported during the entire survey.

Although the carotenoid pigments tended to increase with the chlorophyll concentrations, this was not always the case (Figure 5). In winter, especially, the chlorophyll concentrations were relatively much higher than the carotenoids. This may indicate that there were changes in both type and physiology of the population since it is known that with decreasing light, plants, and plankton as well, tend to increase in chlorophyll content.

Pigment production has been expressed on an area basis following the work of Gessner (1949) who showed that equal areas on the land and water are capable of producing the same amount of chlorophyll. Using this method it was possible to compare the pigment produced at various stations within the lagoon. As mentioned above, station 1 was the deepest station, with stations 7 and 8 the most shallow. Converting chlorophyll *a* from the amount per cubic meter to the amount per square meter (the quantity of chlorophyll beneath a square meter of illuminated surface

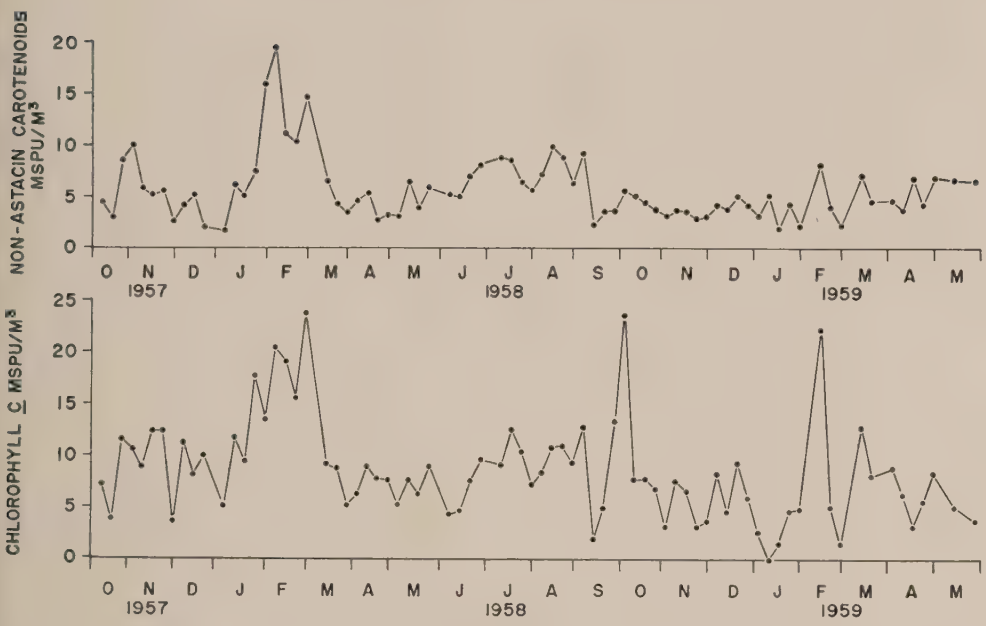

FIGURE 5.—Variation in weekly means of chorophyll *c* and non-astacin carotenoids.

equals the chlorophyll per cubic meter times the depth of the water column in meters), the same amount of incident radiation yielded more pigment at the head of the lagoon (station 1) than at the mouth (station 7) for most sampling periods (Figure 6). Values at sta-

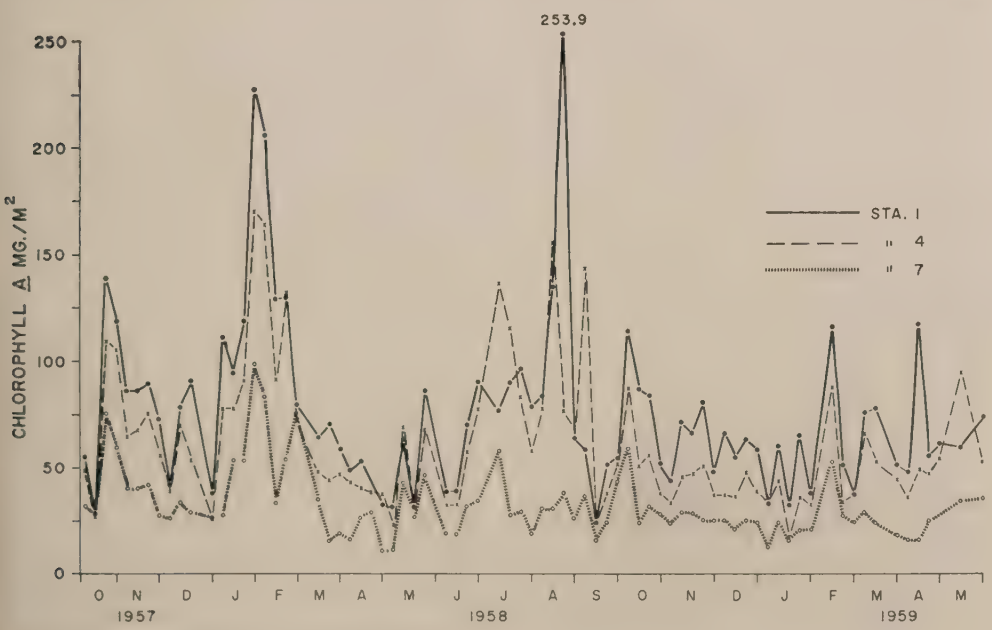

FIGURE 6.—Station variation in chlorophyll *a*.

TABLE 3.—*Variations among stations for period of observation*

Station	Mean chlorophyll *a* (mg/m^3)	Standard error of mean	Range (mg/m^3)	Mean chlorophyll *a* (gm/m^2)
1	18.50	1.0	2.2–84.1	0.08
4	18.95	0.98	5.0–72.2	0.07
7	15.25	0.75	3.0–51.5	0.04

tion 4, in the middle of the lagoon, were intermediate. Table 3 gives the station variations on both volume and area bases.

Although the differences between stations 1 and 4 are not significant on an area basis, those between stations 1 and 7 and between 4 and 7 are highly significant. This is true for chlorophyll *c* as well, but the differences in mean values for the plant carotenoids (non-astacin type) are not significant. These facts together with variations in chlorophyll *b* and *c* previously cited further indicate the dissimilarity in production of the various segments of the lagoon. Although the spring bloom was found in all stations of the lagoon, the late summer bloom (August 1958) was largely limited to the upper segment of the lagoon (stations 1 to 4) in which the highest chlorophyll concentration of the survey was found.

Several factors may have influenced this gradient in production. First, the stations themselves varied in depth so that even at times when the pigment per unit volume of water was similar, the pigment per square meter was almost twice as great at station 1 as at station 7. Second, there was a correlation with change in tide. A comparison of the occurrence of a chlorophyll gradient along the length of the lagoon and the tidal conditions (as recorded at Fort Point, approximately one-half mile from the lagoon proper) showed that gradients were steeper and occurred more often when the tide was changing, and that gradients were weaker and less frequent with standing tides. Station 7 was obviously far more subject to both tidal and current action than the stations nearer the head of the lagoon and was less apt to receive the enrichment from the drainage of the surrounding marsh than station 1. Since it was likely to be more turbid than the other stations due to this tidal action, there may have been an effective decrease in the amount of light reaching the area as well as a dilution due to the influx of poorer Gulf waters. The combination of these factors may explain why this station appeared to be a poorer producer than those along the upper reaches of the lagoon.

There were no data on turbulence, thermal stratification, or nutrient cycles in East Lagoon which would further explain the differences along the length of the lagoon or the periods of bloom. A study of the nutrients in the lagoon was made for a single 24-hour period during July 1958. The inorganic and total phosphorus had values of about 2.5 mg at. $/m^3$. There was some evidence that station 7 had slightly less phosphorus than the upper stations (about 0.1 mg at. $/m^3$ during the period of study). Station 7 also showed less chlorophyll than either stations 1 or 4, with station 1 having not only the greatest amount of chlorophyll but also showing an increase in chlorophyll during the midmorning followed by a decline toward darkness. These samples were taken 1 foot below the surface rather than from the entire water column.

A comparison of the phytoplankton data with zooplankton data collected simultaneously indicated similar differences among stations along the lagoon, although the gradient was apparently reversed. Station 7 was by far the richest in production of zooplankton, with stations 1 and 4 similar to one another but much poorer producers. A small peak of zooplankton abundance was evident in December 1957, following the October and November phytoplankton bloom, but there was no apparent increase immediately following the very large peak in late January and February (Fleminger, 1959). On the contrary, the zooplankton began to increase late in April and May when the phytoplankton (as judged by the pigment concentrations) was on the wane. The zooplankton population, in fact, began to die out during the late summer when the phytoplankton was again reaching periods of bloom. Both declined during the midwinter of 1958–59 and then showed an apparent peak in February of 1959. It has been postulated that grazing plays a large part in the decrease of phytoplankton (Riley, 1946; Riley and Bumpus, 1946), and during the summer months this would be indicated both by large zooplankton populations at the time when phytoplankton was apparently low and by the inverse relationship of phytoplankton and zooplankton along the length of the lagoon.

Physical factors may also influence the genesis of the blooms noted above. Solar radiation itself did not appear to have a direct correlation with pigment production except during one period of observation. There was apparently a more direct relation with rainfall (Figures 2 and 7). Although a period of

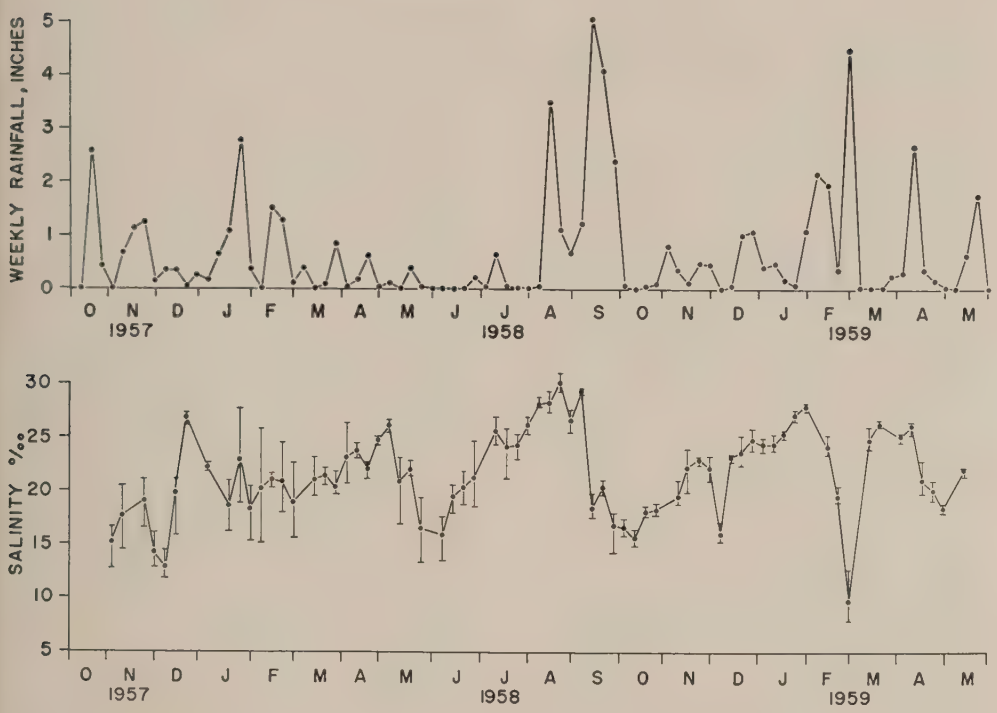

FIGURE 7.—Total rainfall for the Galveston area and mean salinity, East Lagoon.

heavy rainfall alone may not be sufficient to bring about a bloom, rainfall was probably a necessary condition as each bloom was either preceded by (not more than a week) or coincided with periods of relatively heavy rainfall. Further, chlorophyll was minimal during the weeks and months when rainfall was low. The immediate effect of hurricane conditions was a decrease in pigment, due in all probability to the dilution and replacement of the lagoon water by both rain and drainage of the surrounding areas and from the Gulf influx. The hurricane was followed within a week, however, by an increase in pigment concentration. Smayda (1957) has noted the same condition in Rhode Island following the hurricanes of the 1954 season and attributed the immediate appearance of the phytoplankton blooms to an increase in phosphate and iron concentrations. Whether these particular enrichments occurred in the lagoon was not ascertained, but it does seem likely that there was enrichment due to the large influx of drainage water from the surrounding marsh and from the river discharge.

Salinity generally was correlated with rainfall and with season. Values ranged from 8.0 parts per thousand following a heavy winter rain to 31.2 parts per thousand during the late summer. The mean salinity for the entire lagoon for the period of observation was 20.8 parts per thousand.

DISCUSSION

It is necessary to view all results such as these with some caution. When samples are taken several times during the week, conclusions are more firm than when sampling is less frequent. As Rodhe (1958) says concerning the C^{14} method (and it is equally applicable to this type of determination):

> The conclusion that can be drawn . . . is that a sampling frequency as high as once a week need not warrant a true picture of temporal succession. . . . Under such circumstances, we get *one* picture on the basis of samples taken every Monday, but perhaps should achieve quite different peaks and feet in a curve derived from samples taken on Tuesdays, etc. . . . Straight lines connecting weekly dots . . . cannot be regarded, *a priori*, as representative of the course of events during the other six days of the week, neither for the sampling station nor for the lake as a whole. In general, therefore, when

we have to illustrate the seasonal succession, histograms are preferable to smooth or broken curves which easily give the impression of more complete information than the primary results permit.

As mentioned above, the curves given in this paper are averages of all stations for all collections during a given week. Variations in daily means of chlorophyll need not be representative of actual population changes in the lagoon since chlorophyll content changes with the physiological state of the organism, being influenced by nutritional state (lack of essential minerals such as iron), amount of available light, etc. In addition, Rodhe (1958) has demonstrated that chlorophyll content may undergo vast changes from day to day, sometimes of the order of several hundred percent, so that it would be preferable to show actual daily station data. This method would emphasize the fact that frequency of sampling markedly influences the weekly means. Let us compare the two spring blooms, for example. In 1958, samples were taken almost daily so that the weekly average presumably includes the highest chlorophyll values attained during the flowering. In 1959, however, only three stations were being sampled and these at somewhat irregular intervals so that the highest value recorded may not have been the true peak. Since flowerings are notably patchy and occur and diminish with great rapidity, particularly in warmer waters such as those found in the Gulf areas, productivity cannot be accurately quantified unless frequent and regular samples are obtained. Seasonal cycles, however, will be evident.

Seasonal cycles in East Lagoon indicate blooms in January or February and again in October–November with minima in December–January and again in April–May. Atkins and Parke (1951), Atkins and Jenkins (1953), and Jenkins (1955) have reported cycles based on monthly surface samples from the English Channel with maxima in March or April, followed by a decline to a summer minimum and a secondary maximum in September or October. Riley (1946) and co-workers have described similar cycles in Georges Bank and Long Island Sound. In Long Island Sound (Riley and Conover, 1956; Conover, 1956) there was an annual cycle characterized by a large late-winter flowering, with lower values throughout the spring and summer, small sporadic flowerings in summer and early fall, and minimal populations in late fall and early winter. All three studies show similar cycles although the exact time of appearance of the late-winter bloom is dependent upon the latitude.

Wide ranges in chlorophyll content have been reported. East Lagoon has yielded a maximum chlorophyll *a* of 84.6 mg/m^3 for the entire sampling period, with a mean of 17.6 mg/m^3. Marshall (1956), in studies of Florida coastal waters, reported a maximum of about 14 mg chlorophyll *a*/m^3 in Alligator Harbor and a mean of 4.3 mg/m^3. Both are considerably below the values reported here. Even the value of 30.7 mg/m^3 found by Marshall in the midst of a bloom of *Gymnodinium breve* is considerably below the values determined in the midst of blooms in this study. In the Tortugas, Riley (1938) found a mean of 0.33 mg/m^3 of chlorophyll *a*, but these analyses covered only a 2-week period, from July 18 to August 2, when both from my data and from the data of Marshall (1956) it would appear that chlorophyll concentration may not be at its height. Again, Riley (1939) reporting on the western North Atlantic in May and June of 1939, noted that the tropical waters had a maximum of 2.5 mg chlorophyll/m^3 to the 3.6 mg/m^3 of the more northern waters. In Long Island Sound (Riley and Conover, 1956; Conover, 1956) the mean chlorophyll *a* value was considerably lower than that in the enclosed water of East Lagoon, with a maximal value for the years 1952 through February 1954 of only 30 mg/m^3.

Plankton production data from southern regions are somewhat scarce. Odum, McConnell, and Abbott (1958) have reported chlorophyll per square meter for several plankton communities in Texas. Their work indicates that the Texas bays generally yield from 0.043 to 0.200 g chlorophyll *a*/m^2 with a minimum of 0.002 g/m^2 in the Laguna Madre. East Lagoon has given values ranging from 0.044 to 0.37 g/m^2. The latter value, in the midst of a plankton bloom (euglenoid), compares with bloom values from various more northern regions ranging from 0.10 to 0.6 g/m^2 (Odum, McConnell, and Abbott, 1958). Generally, pigment concentrations in East Lagoon may be considered to be higher than those reported by other workers in more open waters, though the maximal concentrations do not reach those reported by others in the midst of special types of plankton blooms.

Organic productivity in the lagoon may be compared with that found in other environ-

ments, following the equation of Ryther and Yentsch (1957):

$$P = \frac{R}{k} \times C \times 3.7$$

where P is productivity in grams carbon per square meter per day, R is a radiation factor found from the graphs of Ryther and Yentsch (1957), k is the extinction coefficient of the water, and C is grams of chlorophyll per cubic meter. Assuming an average radiation of 350 gm cal/cm for the period of observation, an average k of 1.7 (estimated from the average Secchi-disk readings by the method of Poole and Atkins, 1929), and using the mean chlorophyll *a* for the lagoon of 17.6 mg/m^3, there was an average production of 0.27 g carbon/m^2 per day or 0.5 g dry organic matter/m^2 per day. The maximal productivity was 1.74 g C/m^2 per day, or assuming the organic product to be 50 percent carbon, 3.5 g dry organic matter/m^2 per day. These approximations compare with maxima for a single day reported by Ryther (1959) of 2.8 g/m^2 per day in the Sargasso Sea with an annual average of 0.9 g/m^2 per day in Long Island Sound.

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SEXUAL BEHAVIOR OF THE OYSTER DRILLS: EUPLEURA CAUDATA AND UROSALPINX CINEREA[1]

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The observations reported herein are part of an extensive study of the biology of *Urosalpinx cinerea* (Say), the smooth oyster drill, and *Eupleura caudata* (Say), the rough oyster drill, which is in progress at our laboratory. Results of studies of other aspects of the behavior and ecology of these predatory snails will be reported as they become available.

Little is known of the copulatory behavior of dioecious marine gastropods. Though Stauber (1943) reported a partial pairing of *E. caudata,* pairing of *U. cinerea* has never been described. Our studies show that pairing of both species is a complex process involving fairly intricate behavior of both sexes.

Copulation of Eupleura caudata. According to Stauber's (1943) description of a partial mating of *E. caudata* the male mounted the right side of the female and formed the anterior part of his foot into a copulatory groove through which the penis was ex-

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FIG. 1

FIG. 2

Eupleura caudata (Say). Fig. 1, male and female in copula. Fig. 2, two males attempting copulation with one female.

tended into her mantle cavity. Even though disturbed repeatedly this pair copulated intermittently for 21 days. Our laboratory observations of pairing of captive *E. caudata* confirm and enlarge upon those of Stauber. Eighty-one separate pairings were observed but because the average time each couple was together was extensive and coitus occurred intermittently, only two copulations were seen from beginning to end.

Prior to coupling, the female usually moved about the aquarium walls and finally assumed a stationary position with her siphonal tip upward. Pairing also occurred in horizontal positions on oysters, or on the aquarium bottom, or rarely, on the walls. The mantle cavity was then exposed by allowing the shell to hang down and away from the posterior part of the foot. Though in most cases a male (or males) had already assumed a position upon the shell of the female, several unpaired females also exposed their mantle cavities in the same fashion prior to copulating and probably this behavior is normal precopulatory activity. Following this the male often moved about on the female's shell for a short time but eventually assumed a stationary position on her right ventral surface slightly posterior to the mantle cavity with his siphonal cavity pointing in the same direction as hers (Fig. 1, p. 6). The foot of the male extended to the rim of the mantle cavity and a copulatory groove formed in its anterior surface through which the penis was protruded into the mantle cavity and presumably the vagina, though that orifice was always hidden from view by the shell. On termination of copulation, the female often twisted from side to side and opened and closed the cavity opening. Similar twisting behavior has been observed in other gastropods apparently attempting to dislodge predatory snails, *Odostomia,* from their shells (Allen, 1958). The male then withdrew and either remained in position or moved about on the shell of the female or to the substrate.

E. caudata usually remained in position and copulated intermittently for extensive periods, often up to 48 hours. Two pairs copulated continuously for 2 hours 45 minutes ± 15 minutes and 3 hour 39 minutes ± 10 minutes, and a third for 5 hours ± 10 minutes, but all were paired longer. Another pair copulated intermittently for a total of at least 8 hours 48 minutes over a period of two days, during which the male maintained his posi-

tion on the female. A marked pair copulated 11 times in five months. During this period the pair often separated and the female paired with other males.

Eupleura caudata showed marked promiscuity. Of 29 marked pairs, 12 females copulated with more than one male and 15 males with more than one female. One male copulated with 6 different females and one female accepted 5 males throughout the season. Although these are observations on drills confined in running-water aquaria and cages, there is little reason to doubt that, depending on density and movement, similar promiscuity occurs in nature.

Usually, males were smaller than their consorts (48 males: mean height 18.7 mm., range 14.9-23.5 mm., standard deviation 2.3; 44 females: mean height 22.6 mm., range 17.5-28.9 mm., standard deviation 3.2).

Seasonal periodicity of copulation was determined in outside cage experiments and running-water aquarium observations. Though the frequency of observation was not always constant throughout the year, the number of pairings seen in aquaria per month roughly corresponded to those in more careful cage experiments. In 1956 pairings were recorded as follows: March-6, April-14, May-15, June-3, July-9, August-1, September-1, October-9, November-1, and December-1. The first occurred on March 7 (12.9°) and the first peak occurred in late April and early May. A second peak came in July, comparatively few pairings occurred from July through September, but an increase took place in the last part of October. Copulation ceased after December 10 (10.3°C). The lowest temperature at which pairings were observed was 10.3°C, the highest 28.4°C. Also in 1956, 30 females and 30 males, caged in a single large compartment, were examined every two days between 1400 and 1700 hours. Onset of the mating period was not observed because the experiment was established too late in the season. Pairing was first seen in late April at 13.7°C, reached a peak on June 7 at 23.7°C, and ceased on July 7 at 26.1°C, (Figure 3). A late wave of 28 pairings, about one-third as intense as the spring wave, began at the end of September (21.7°C) and ended November 11 (16.4°C.) Observations made two or three times a week during the winter of 1956-57 revealed no copulatory activity but this was expected because all other

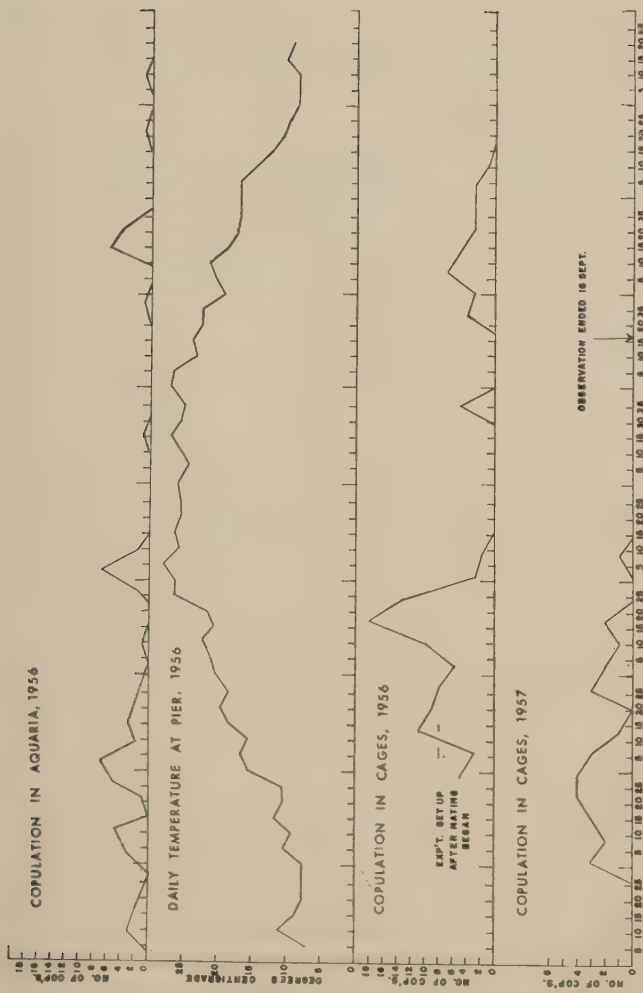

FIGURE 3. SEASONAL COPULATION OF E.CAUDATA

overt activity had ceased. Observations in the first half of the summer of 1957 on two cage compartments containing 45 specimens each (sex ratio of entire sample, 50 females to 40 males) indicated that copulation was less intense than in 1956. Pairing was first observed on April 4 (11.1°C). There was no distinct peak

and after the week of May 6 activity slowed and ceased on July 6 (26.1°C). Most activity occurred slightly earlier than in 1956, probably as a result of earlier warming. No observations were made in late summer.

Little diurnal periodicity was noticed and nocturnal activity was not investigated. Of 56 pairings, 23 (48 per cent) were completed before 1200 hours and 29 (52 per cent) occurred after 1200 hours. Because observational effort varied somewhat these data are not precise, though they are probably indicative of general conditions and comparable to those pertaining to *U. cinerea* gathered in similar fashion, see below.

On two occasions, pairs of males were observed *in copula.* Careful external examination and studies of gonad smears showed all four animals to be normal males with no detectable female characteristics. Five trios *in copula,* each composed of a female and a male in the usual position with an extra male in copulatory position on the first male, were also observed in aquaria. The extended penes of both males were seen twice. Usually the male next to the female copulated with her while the intromittent organ of the second male extended into the mantle cavity of the first, but at times both males attempted copulation with the female (Fig. 2, p. 6). Copulations involving two functional males, the middle one acting as both male and female, and another female has been reported for the hermaphroditic species, *Lymnea stagnalis,* (Crabbe, 1927) but never for dioecious gastropods. Once a quartet with 3 males, all situated chain-fashion on a female, was observed. The penes of at least two of these males were extended into the mantle cavity of the animal before them. In dioecious animals, like drills, these aberrant copulatory groups have little reproductive significance, but seem to support the hypothesis of exocrine stimulation or attraction of males to females. Possibly the males were attracted to the females, or to each other, by release of female exocrine in the vicinity and, without being able to discriminate further, established and maintained contact with each other.

Copulation of Urosalpinx cinerea. Observations of 76 pairs of *U. cinerea* showed their copulatory behavior to be generally the same as that of *E. caudata,* but with several distinct differences. The female usually assumed a stationary position with her

siphonal tip upwards, allowed the shell to fall away from the substrate, thus exposing the right rear corner of the mantle cavity and twisted the shell from side to side several times in a sort of "precopulatory dance." Most often a male was already on the female's back when this precopulatory play was observed, but several times males appeared to be attracted from afar to the demonstrating female. Sometimes unattached males, often several at a time, were attached to a demonstrating female or copulating pair, possibly drawn to the receptive female or the pair by some stimulus, probably an exocrine. Following the precopulatory demonstration by the female the male assumed a position on her right ventral side, formed a copulatory groove of the anterior portion of his foot and inserted his penis through the groove into the female's mantle cavity. On completion of coitus, the intromittent organ was withdrawn, and in contrast to the slow separation or intermittent resumption of *E. caudata,* the male moved quickly away. The shortest complete copulation observed lasted 4 minutes, the longest 32 min. Including preplay time, one complete pairing occupied one hour and 25 minutes, but actual copulatory contact required only 11 minutes. Usually *U. cinerea* copulation occupied only 3 to 4 minutes. This characteristic short contact, seldom more than 4 or 5 minutes, probably explains why *U. cinerea* mating has not been previously reported.

According to our observations, only one pair of 20 marked pairs recopulated and the pairings were 1½ months apart. Of the marked pairs 7 males and 2 females coupled with different mates. Thus, *E. caudata* seemed more promiscuous than *U. cinerea.* However, the incidence of promiscuity in *U. cinerea* may be actually greater than these data indicate because of the unlikelihood of observing its brief sexual contacts as readily as the much longer ones of *E. caudata.*

The male is usually the smaller of the pair: 41 pairing Seaside (from the ocean coast of the Eastern Shore of Virginia) males averaged 29.8 mm. in height, range 19.5-38.7, standard deviation 5.1; 46 females averaged 34.4 mm. in height, range 21.9-44.6 mm., standard deviation 4.7; six York River males averaged 19.3 mm. in height, range 16.5-24.6 mm. and five females averaged 19.5 mm. (17.3-21.2 mm.).

Pairing was seen in late October and early November, 1955,

until the temperature dropped to 13.7°C. In 1956, it began on February 29 (8.2°C., increased in March with 10 pairings, reached a peak in April with 17 pairings, and diminished in May to three pairings (20.3°C). Pairing was not observed again until October, (20.8°C), none in November and 2 on December 7 (11.5°C). Of 59 pairings, nine (15 per cent) were observed before 1200 hours and 50 (85 per cent) after 1200 hours. In contrast to *E. caudata, U. cinerea* seems to exhibit marked preference for the afternoon.

Two pairs of structurally normal males were observed *in copula* and, on another occasion, two males were observed copulating with one female.

Sperm viability and storage. One *U. cinerea* male, forcibly separated from a female, exuded sperm in a continuous, viscous stream, thus indicating that discrete spermatophores are probably not employed. Examination of seminal receptacles of at least 50 females of both species support this conclusion. Seminal receptacle smears of two females taken immediately after copulation contained immotile sperm while those in another were motile; therefore, it is not clear whether the sperm are immotile when passed. Microscopic examinations of seminal receptacles of several hundred individuals of both species revealed that many mature females contained fully or partially motile sperm at all times of the year though the sperm in some were entirely immotile. Whether they are stored in the motile condition is not clear because the mechanical action of smearing may have stimulated the sperm to activity. Apparently spermatozoal energy is sustained in some way, either through conservation of energy by immotility or special nourishment because both species can store viable sperm for considerable periods of time.

Stauber (1943) reported that a *U. cinerea* female isolated from April to October of the same year deposited egg cases containing viable embryos through the period. In our experiments 4 females isolated in November and December of 1955 produced viable eggs the following spring and summer. Of these, one deposited in May after 5 months, two spawned in August, after somewhat less than 9 months, and one in September after 9 months. Two post copula *E. caudata* females isolated in 1955 produced egg cases through 1956 and into 1957, but the embryos produced in 1957

did not develop. Unless parthenogenesis occurred—which is most unlikely—or the so-called "embryos" included in these 1957 egg cases were merely unfertilized ova and not really embryos at all, the sperm must have been vigorous enough to affect fertilization even after a storage period of over 14 months. In any case, however, the embryos (or unfertilized ova) produced in 1957 failed to develop even though handled in the same fashion as others which survived. Eight other females, isolated in late fall or early winter of 1956 produced viable cases for periods of at least six months after isolation.

Discussion. Several points of biological interest have arisen during the present study. Because of the nature of the photo receptive organs it is doubtful, but not certainly so, that the precopulatory "dance" or movements of the female attracts the male. More feasible is the chemical stimulation of the male by the female. If female oyster drills actually attract males during their "premating ritual" by release of an exocrine, such a chemical might be useful as an experimental or control tool because it is probably highly specific and powerful enough to be effective in extreme dilution.

It has been shown that females of both species are able to store sperm in their seminal receptacles for extensive periods. The mechanisms by which they are sustained should be of interest in studies of cell culture and nutrition.

Oyster drills are promiscuous and have the facility for sperm storage; therefore, unless sperm from previous pairings are discarded or resorbed completely before another mating occurs, a female contains viable sperm from several different males in her seminal receptacle. Under these circumstances, embryos produced therefrom might have different paternal hereditary materials. Thus, differences in rate of embryonic development, time of hatching, appearance, etc. may be due to varied paternity and not the usual genetic difference found among siblings. Until the precise nature of sperm storage, syngamy and egg case formation is understood, experimenters working with drill embryos cannot safely assume that all embryos in a unimaternal cluster or even a single egg case are of the same parentage.

Summary

1. *Eupleura caudata* and *U. cinerea* exhibited fairly complex

mating behavior involving definite precopulatory movement patterns by the female, stimulation of nearby males, possibly by exocrine activity, assumption of relatively constant copulatory positions by both sexes and copulatory groove formation by males. Females often twisted violently immediately prior to cessation of copulation.

2. *Urosalpinx cinerea* completed copulation in a matter of minutes, but *E. caudata* often persisted intermittently for days, remaining in position all the while.

3. *Eupleura caudata* was apparently more promiscuous than *U. cinerea* but possibly this disparity may have been a function of a species different in frequency of a pairing, *i.e.,* if *E. caudata* normally pairs more often, its comparative incidence of promiscuity would naturally be greater. Or, it may also have been a function of the length of time that pairing consumes. For example, *E. caudata* pairing takes much longer than *U. cinerea* (12 to 20 hours vs. 3 to 4 minutes or up to 200 times longer); therefore, *U. cinerea* copulation would more easily be overlooked, resulting in a numerical bias in favor of *E. caudata* in any comparison of frequency of pairing.

4. Though *U. cinerea* paired at lower temperatures than *E. caudata* (8.2°C vs. 10.2°C), mating activities of both increased during April. *U. cinerea* ceased copulatory activity in June while *E. caudata* persisted through the first week in July before stopping temporarily. Both resumed mating activities in September which increased in October, diminished in November and ceased altogether in early December.

5. In our laboratory aquaria, *U. cinerea* copulated more frequently in the afternoon and evening while mating activities of *E. caudata* were more evenly distributed throughout the day.

6. Females of both species stored viable sperm in their seminal receptacles for periods of at least 6 to 9 months.

7. Several items of general biological interest, sperm nutrition and multiple paternity of embryos within a single egg case, etc., have been discussed.

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ROBERT W. HOLMES AND JAMES M. SNODGRASS

A MULTIPLE-DETECTOR IRRADIANCE METER AND ELECTRONIC DEPTH-SENSING UNIT FOR USE IN BIOLOGICAL OCEANOGRAPHY

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A Multiple-Detector Irradiance Meter and Electronic Depth-Sensing Unit for Use in Biological Oceanography[1]

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ABSTRACT

The underwater irradiance meter or submarine photometer described here is designed to operate in the upper 100 to 150 m. It permits direct measurement of the downward blue-green irradiance (480 mμ) to a depth of 100–120 m on a clear day in water with an attenuation coefficient in the blue-green region of the spectrum of approximately 0.04/m. The meter can accommodate as many as five individual detector units as well as an associated depth-sensing element. The detectors are cosine flux collectors, equipped with a dry disk, self-generating, barrier layer cell. Any single detector unit may be readily oriented up, down, or horizontally. Selection among the detectors is made by energizing the switching mechanism with a push button. Their output is measured in the vessel's laboratory with a damped multirange microammeter of low internal resistance. The associated depth-sensing unit is transistorized and battery-powered and is capable of measuring depth down to 200 m with an accuracy of $\pm 2\%$ in the 50–200 m range. The unit is stable, rugged, and relatively insensitive to temperature changes in the range between 2° and 25°C. The detector and depth signals are carried by a two-conductor electrical cable, which also supports the instrument. A sea return is utilized in the detector unit switching assembly.

Introduction. The need for a versatile irradiance meter for use in connection with studies of phytoplankton ecology has been plain for some time. Marine biologists and biological oceanographers studying phytoplankton and littoral alga photosynthesis are now frequently measuring attenuation coefficients and light levels; they require more complex and precise information as their studies become more elaborate.

[1] Contribution from the Scripps Institution of Oceanography, New Series. This paper represents results of research carried out by the University of California under contract with the U.S. Bureau of Commercial Fisheries.

[2] The authors wish to acknowledge the information received from John Tyler, research physicist of the Visibility Laboratory of the University of California, Scripps Institution of Oceanography, La Jolla, concerning the design and characteristics of the flat plate collectors used in the detector unit.

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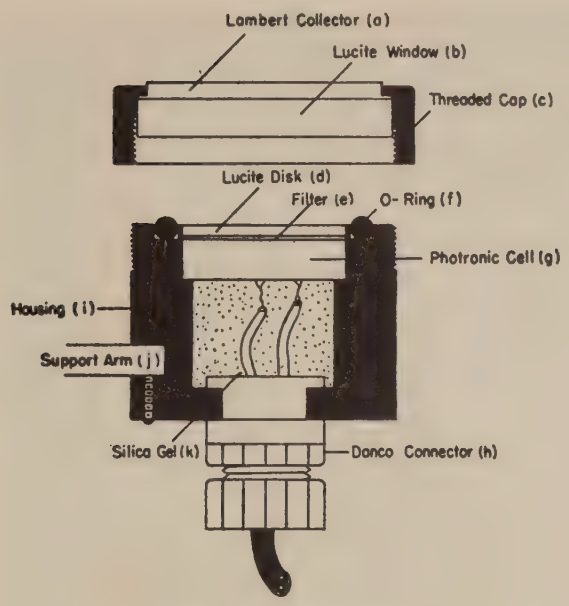

Figure 2. The detector unit.

cap until a seal is obtained between the O-ring (f) and the lucite window. The color and/or neutral filter (e) may be placed above the photocell (g); when gelatin filters are employed, they are held in contact with the photocell by a lucite disk (d). Silica gel (k) placed in the space below the photocell prevents window fogging and moisture damage to the gelatin filter. The electrical leads from the photocell are taken through the housing in a nylon stuffing tube (h) (Danco, Size 1, Danielson Mfg. Co., Danielson, Conn., packing assembly for the tube, Dorn Equip, Corp., Boston, Mass.); they terminate in a Joy plug (No. X8104–63, Joy Mfg. Co., Compton, Calif.).

The particular cosine collector used in this instrument is fabricated from milk-white translucent plastic (Rohm and Haas, Plexiglass 2333, Philadelphia, Pa.), the surface of which has been carefully abraded with carborundum (Grit No. 180) to give it cosine-collecting properties when submerged. There are of course other ways to build cosine collectors; the important thing to know is the properties of the flux collector.

Hermetically sealed barrier layer (dry disk) self-generating cells (Model 856RR), manufactured under the name Photronic Photoelectric Cell (Weston Electrical Instrument Corp., Newark, N.J.), have been employed in these detectors. These cells have proved stable and rugged enough for use in this type of work.

The meter described here is the result of the authors' experience over seven years in measuring attenuation coefficients and developing instrumentation. This particular instrument has been in intermittent use and under modification for two years. The present design has proved to be reliable and of general applicability for high seas research in which the objective is to study, in the field, the role of light in photosynthesis.

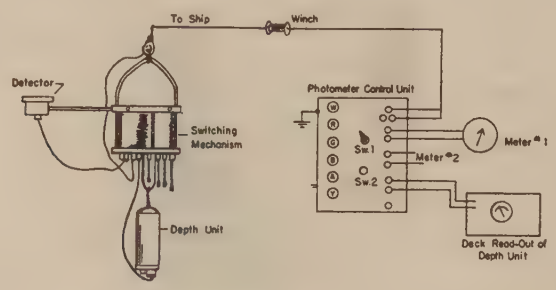

Figure 1. The irradiance meter and depth-sensing unit.

The meter (Fig. 1) is a single or multidetector unit capable of measuring the irradiance on a flat surface oriented at any desired angle. The individual flux collectors may be oriented in advance to measure the attenuation coefficient for downwelling or upwelling irradiance. By combining these two measurements it is possible to compute the reflectance at an imaginary horizontal plane in the sea, or to obtain the ratio of the irradiance on a plane facing the sun to that on a plane facing away from it. By proper selection of optical filters, the instrument can be set up to measure either the same optical property for a number of band widths nearly simultaneously or several optical properties for the same band width.

Irradiance is easily measured and by its use the results from different areas and regions can be standardized and compared. Furthermore, attenuation coefficients k calculated from the irradiance data using the following equation

$$k_\lambda = \frac{2.30}{L}(\log I_{\lambda,k} - \log I_{\lambda,k+L})$$

are useful in biological and physical oceanographic studies (Holmes, 1957 or Sverdrup, *et al.*, 1942).

The Detector Unit. Each detector unit (Fig. 2) consists of a photocell housing (i) and a threaded cap (c). The latter accommodates the Lambert or cosine collector (a), elevated about 1 mm above the cap and the lucite window (b). A watertight seal between these components is effected by rotating the threaded

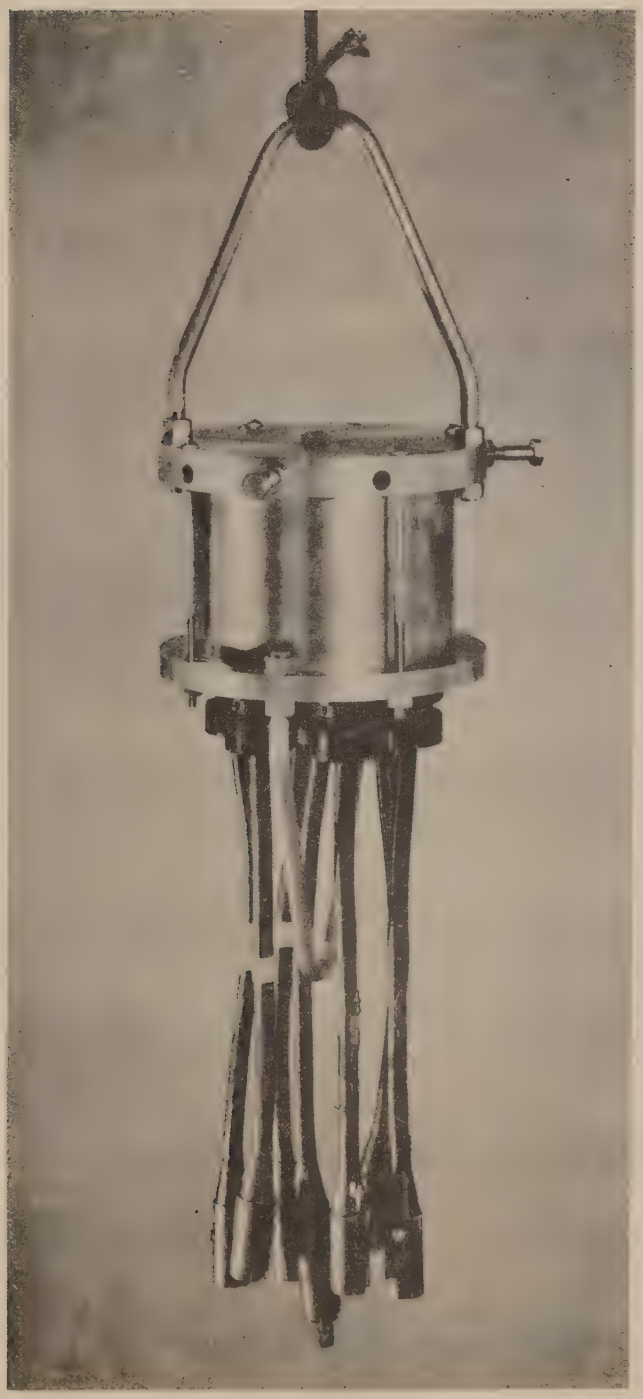

Figure 3. The underwater switching unit.

Figure 4. The deck control unit.

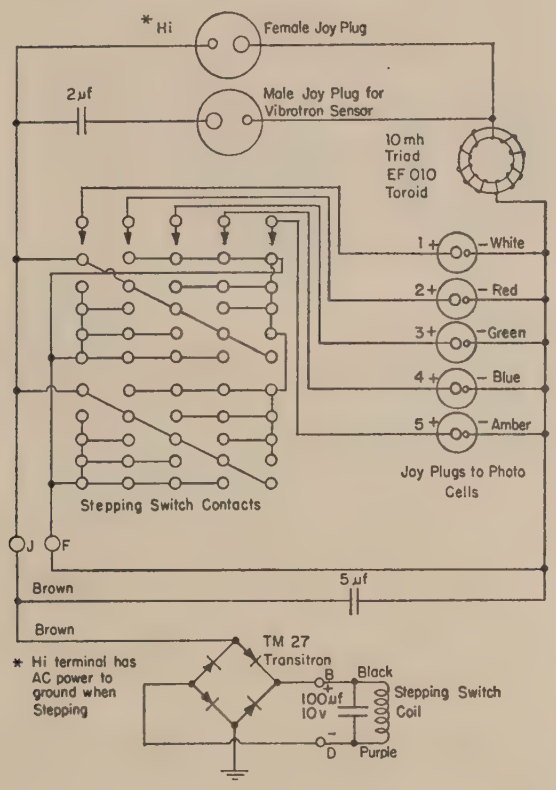

Figure 5. The underwater switching unit. Schematic diagram.

Switching Mechanism and Deck Control Unit. The detector units are mounted on stainless steel rods, approximately 40 cm long, which are inserted into holes provided on the top plate of the underwater switching unit (Figs. 1, 3). The orientation of the detectors may be adjusted and maintained by utilizing the Allen set-screws mounted in either the detector or the switching mechanism. Electrical continuity from the detectors is achieved by means of connecting the Joy connectors (Fig. 3).

The underwater component of the switching mechanism consists of an oilfilled brass housing which contains a rotary stepping switch (Type 44, Automatic Electric Sales Corp., North Lake) and associated equipment (Figs. 3, 5). Seven outlets pass through the bottom of the housing; five for use with detectors, one to connect with the depth element, and one to connect to the cable that supports the instrument and carries the signal to the photo-

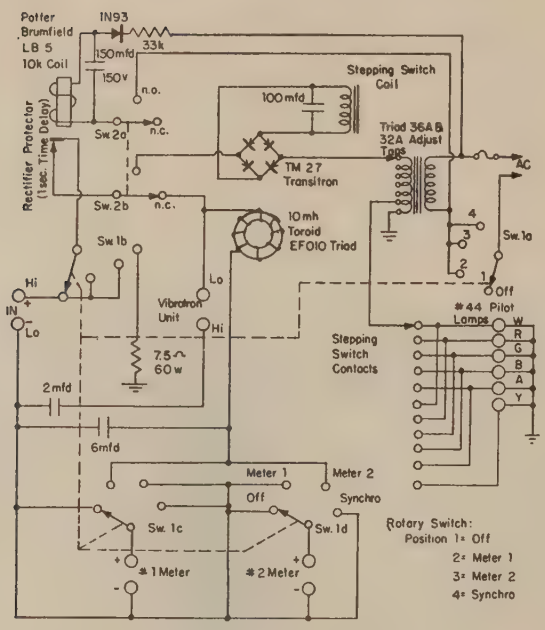

Figure 6. The deck control unit. Schematic diagram.

meter winch, whence the signal goes to the deck control unit. The selection of the particular detector is controlled by means of a push button on the deck control unit ("Push to Step", Sw. 2, Figs. 4, 6).

The deck control unit (Figs. 4, 6) is energized from 115-volt, 60-cycle, AC power. When the instrument is turned on, one of six panel lamps (the sixth has no detector associated with it) indicates which of the five detectors are connected to the meter or recorder jack located on the right-hand side of the instrument. Provision has been made for the use of two meters or of one meter and/or a meter-amplifier combination by the inclusion of a second outlet on the control unit. The selection of these outlets is controlled by a switch mounted in the middle of the control unit panel above the energizing (Push to Step) button.

There are several fundamental limitations to the mechanism as it is at present designed. First, a maximum of 4 ohms is all that can be tolerated per conductor between the deck and underwater units. If the resistance is increased above this limit, the photocell output becomes less linear at high light levels and effectively less sensitive. Further, since a sea return is used and is included in the 4-ohm limitation, the instrument is not designed to be used in fresh

water. Because the sea return is normally less than $^1/_4$ ohm, it is clear that the electrical conductor is essentially the limiting factor.

The circuitry is straightforward, as schematized Figs. 5 and 6 show. Two special features merit mention. The photocells not in use are shorted (as recommended by the manufacturer); and a specific control position is provided on the deck control unit to permit easy and rapid synchronization between the two units if they require rephasing. In addition, a simple filter system is used to prevent any interaction between the depth unit signal, which is AC, and the DC potentials from the photoelectric cells.

Performance of the Meter and Measurement of Attenuation Coefficients. The current generated by a Photronic cell in a constant light field is a function of cell sensitivity, external resistance, and temperature. During routine irradiance measurements, the first two of these factors are constant; only the temperature of the cell varies. Technical information supplied by the manufacturer shows that with an external resistance of about 105 ohms, the output of a cell in a constant light field of 200 foot-candles will vary from −2% to +3% in the temperature range 0–40°C, using 20°C as the reference point. The deviation is less in the temperature range 10–25° (*c* ±1.5%); the data are not corrected to allow for this error.

TABLE I. Linearity of Response of Two Photronic Cells as Determined from Optical Bench Measurements.

	μA Output at 105 ± 1 Ohms						
	Cell No. 8				Cell No. 3		
Log Flux (Theoretical)	4 Feb.	10 Mar.	21 Oct.	29 Dec.	3 Feb.	21 Oct.	26 Dec
0.0	1000	1000	1000	1000	1000	1000	1000
0.1	814	818	820	819	812	820	812
0.2	656	658	660	660	653	660	657
0.3	528	532	535	535	527	535	542
0.4	426	425	430	430	421	424	–
0.5	342	342	342	342	337	342	348
0.6	272	273	275	274	269	274	280
0.7	217	218	218	220	213	222	226
0.8	174	175	175	174	171	174	182
0.9	138	139	138	140	136	139	144
1.0	111	112	105	112	109	112	115
1.1	88.4	87.5	85	88	85.8	87.9	92
1.2	70.4	69.5	69.5	70.1	68.6	70.1	72.1
1.4	44.5	44.2	43	44.6	43	44.2	46.5
1.6	28.3	–	30	–	27.6	28.6	–
1.8	18.1	–	–	–	17.6	18.1	–
2.0	11.5	–	–	–	11.2	11.6	–
2.2	7.3	–	–	–	7.2	7.4	–
2.4	4.6	–	–	–	4.45	4.9	–

The type 856RR Photronic cells are stable in terms of linearity of response. However, since no two cells are identical, it is important if reliable measurements are to be made at high light levels to determine the linearity of response for each cell under the resistance load that will obtain during actual measurements. This may be done on an optical bench or with a series of neutral filters of known transmittance. In Table I, linearity-of-response data obtained at intervals over an 11-month period are given for two type 856RR cells. There is an indication of a slight increase in linearity over the time interval, but this may not be significant.

The flux sensitivity of one of these cells has remained virtually constant ($c \pm 5\%$) for two years.

During routine measurements at sea, the output of the detector unit(s) has been measured with a Rawson multimeter (Model 501, special slow response) possessing five scales (0–50, 100, 200, 500, and 1000 μA), each with an internal resistance of 100 ohms. The meter has been inductively damped so that its response time is on the order of 45 sec. It has been assumed that, under conditions of rapidly fluctuating light levels such as are frequently encountered in the upper 15 m, the damped meter gives an estimate of the average light levels.

Attenuation coefficients may be readily determined providing visible incident irradiance is measured simultaneously with the output of the detector(s) at a series of depths and providing the linearity of the detector element is known.

Under ideal field conditions this irradiance meter gives very reproducible

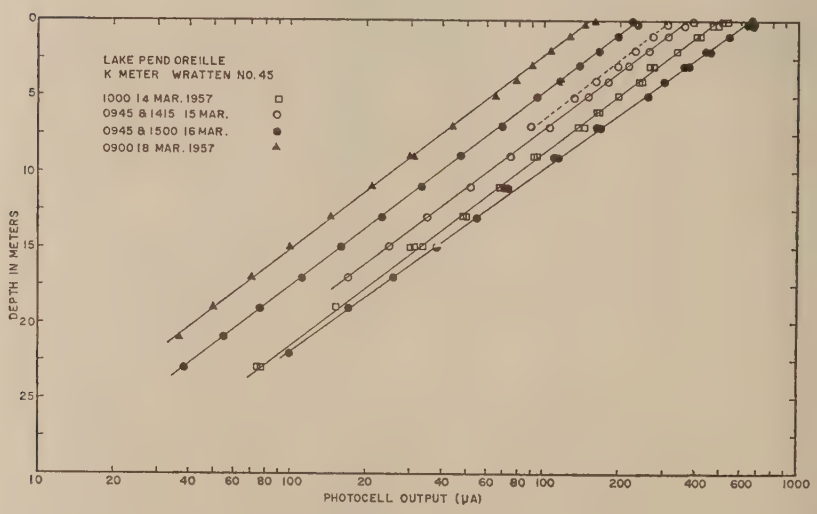

Figure 7. Relative irradiance at different depths. Lake Pend Oreille. Wratten No. 45 filter.

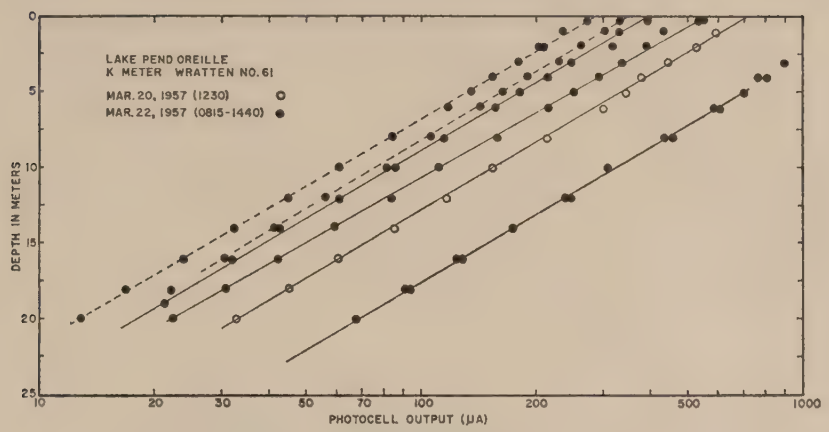

Figure 8. Relative irradiance at different depths. Lake Pend Oreille. Wratten No. 61 filter.

results, as the data presented in Figs. 7 and 8 demonstrate. These data were collected in Lake Pend Oreille, Idaho, in March 1957, with a different switching mechanism but with the same detector and galvanometer mentioned above. Correction for departure in linearity and for changes in incident solar radiation has been made. The corrections for incident radiation were made in such a way that the various curves are not superimposed. Thus the relatively minor departures in slope (the attenuation coefficient) between the eye-fitted curves may be readily seen. The Wratten No. 45 filter has its transmission peak at 480 mμ and the No. 61 at 520 mμ.

Comparable replicate measurement series obtained in the sea show that the k values are more variable than those obtained in Lake Pend Oreille. The vertical oscillations of the vessel and the high wire angles resulting from ship drift or subsurface currents make measurement more difficult and less certain. A typical series of measurements obtained on four separate lowerings of the irradiance meter in the Pacific Ocean about 20 miles west of La Jolla, California, on 1 May 1959 is illustrated in Fig. 9. Conditions were quite favorable during this set of observations: the sky was nearly uniformly overcast, sea and swell were moderate, and wire angles were less than 5 degrees. Corrections similar to those applied to the data in Figs. 7 and 8 were also made. The rather obvious differences in the slopes of these curves in the deeper layers probably are the result in part of inaccurate depth determinations. Had the depth element described in the next portion of this paper been employed, these curves might have become essentially parallel, as were the Pend Oreille profiles (Figs. 7, 8), where depth determinations had essentially no error.

While the sensitivity of the Photronic cell is not particularly high, measurements in the blue-green region (Wratten No. 45 filter) may be made to depths

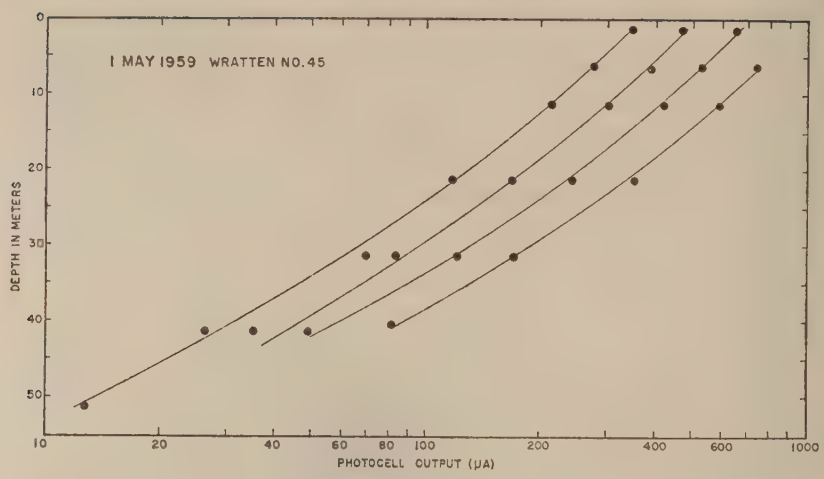

Figure 9. Relative irradiance at different depths. Pacific Ocean 20 miles west of La Jolla, California. Wratten No. 45 filter.

of approximately 100 to 120 m on clear days when the water possesses an attenuation coefficient (in this same spectral region) of approximately 0.04 per meter. Under these conditions about 1.8% of the blue-green light penetrating the sea surface will be found at 100 m depth. A considerable increase in sensitivity of the unit may be easily obtained by amplifying the photocell signal.

The Depth-sensing Unit. In order to measure attenuation coefficients with precision, instrument depth as well as light levels must be measured accurately. Experience gained from examining many irradiance-depth profiles has indicated that depths computed from wire length and wire angle measurements cease to be reliable with wire lengths exceeding 50–60 m if high wire angles (*i. e.*, 40–45°) are encountered. Thus if reliable light measurements deeper than approximately 60 m are desired, the photometer depth should be measured by some other technique. This requirement led to the development of the depth-sensing unit described below.

For convenience in describing it, the component parts of the depth unit are schematized in Fig. 10. The pressure-sensing element (Vibrotron Digital Pressure Gauge, Model 101-12-300, Borg-Warner Controlls Corp., Santa Ana, Calif.) consists of a vibrating wire maintained in a vacuum and driven by a transistorized, battery-powered amplifier. Pressure changes on the end of the wire that is attached to a pressure diaphragm alter the tension of the wire and hence its frequency.

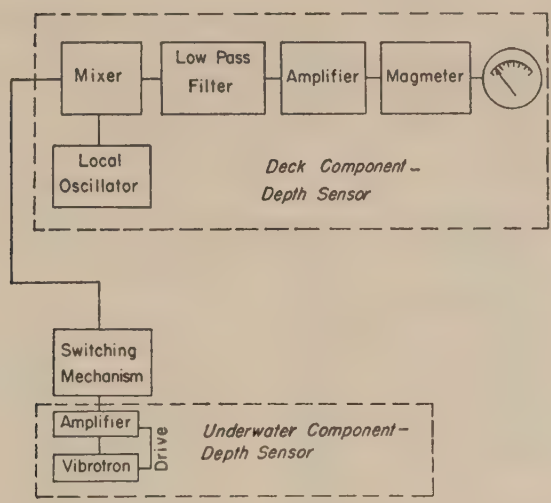

Figure 10. Principal components of the depth-sensing unit. Diagrammatic.

The deck component of the depth-sensing unit is connected to the meter control panel (Fig. 1). The amplified signal from the vibrating wire, coupled into the irradiance meter's switching mechanism, feeds into a mixer, where the local oscillator produces a frequency which corresponds to the Vibrotron zero psia frequency. The resultant difference frequency is fed through a low-pass filter to remove unwanted components and then amplified. The amplified signal passes through a Magmeter (No. F-5161, Airpax Products Co., Balti-

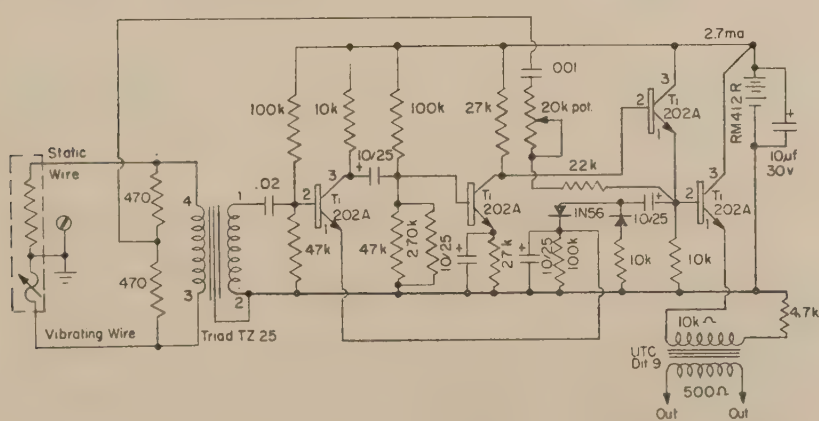

Figure 11. Depth-sensing unit. Wiring diagram of underwater unit.

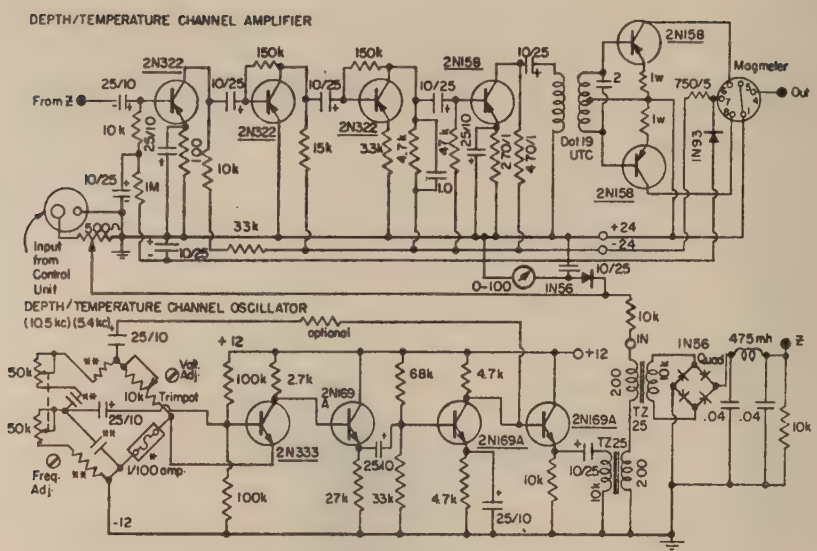

Figure 12. Depth-sensing unit. Wiring diagram of deck unit. * 8 AG Little fuse. ** Values depend on frequency. 904: Texas Instrument or 2N333 G.E. 2N169A; 2N322: G.E. 2N158 C.B.S.

more, Md.) and is then read on a 0–100 μA meter. Figs. 11 and 12 show the wiring diagrams of this circuitry.

Battery life in the deck component is of the order of several hundred hours. The depth component is somewhat underpowered, but battery life normally averages in excess of 10–11 hours with continuous operation at room temperature (18–24°C).

Calibration and Reproducibility of the Depth Unit. The depth unit was calibrated against an Aschcroft 0–600 psi dead weight gauge (type 1300) between 0 and 300 psia. During the test the Vibrotron frequency was also monitored with a Berkeley Eput Meter, Model 554-M. These data are presented in Table II and in part in Fig. 13.

A test of the reproducibility of the depth unit was made at room temperature (25°C) by taking 11 measurements at 5 pressures (50, 100, 150, 200, and 300 psia) after zeroing the instrument at atmospheric pressure. Each set of measurements between 0 and 300 psia was made by progressively increasing the pressure in the increments given above. After each series the pressure was released and the instrument was allowed to equilibrate at atmospheric pressure for a minute or two before beginning the next series. The Vibrotron frequency was also monitored directly with the Berkeley Eput Meter. The data obtained

TABLE II. CALIBRATION OF THE PHOTOMETER DEPTH UNIT (25°C).

	A		B	C
psia	Deck Unit Reading	Vibrotron Frequency	Vibrotron Frequency	Vibrotron Frequency
0	0.0	11108	–	11108
5	4.0	11067	11066	11066
10	5.0	11046	11045	11044
20	8.5	11004	11003	11002
30	11.5	10962	10961	10960
40	14.5	10919	10918	10918
50	17.5	10877	10876	10876
60	20.5	10834	10833	–
70	23.5	10791	–	–
80	27.0 –	10748	10747	10789(?)
90	30.0	10705	–	–
100	33.5	10661	10660	10659
110	36.5	10618	–	–
120	39.5	10574	10573	–
130	43.0 –	10530	–	–
140	46.5	10486	10484	–
150	50.5	10441	10440	10439
180	59.5	10306	10305	–
200	66.0+	10215	10214	10213
240	80.0	10031	10030	–
250	83.5	9984	–	9983
260	87.0 –	9937	–	–
280	93.5	9842	9842	–
300	100.5	9746	9746	9745

in this manner are given in Table III along with the mean value, standard deviation, and coefficient of variation for each pressure series.

A glance at the Vibrotron frequency at each pressure, as read on the Berkeley Meter, shows the high degree of consistency in the results. The deck component of the depth unit cannot be read as accurately as the frequency meter, nor is it as stable, but it is entirely adequate for the purpose for which it was designed. The coefficient of variation is not constant over the pressure range but averages somewhat less than 1%. Thus, for 95% confidence (±2 standard deviations) at room temperature, the depth estimate would be accurate to about ±2%.

The underwater component of the depth unit was found during its design and assembly to be relatively insensitive to temperature changes between 0 and 25°C; and this matter was investigated further in the laboratory with the unit as a whole. In this test the pressure was measured with a 0–300 psi Heise Burdon gauge (No. H-1731) which was found subsequently to need recalibration, but relatively the readings are assumed to be satisfactory. The depth unit was allowed to equilibrate at room temperature (25°C) when readings

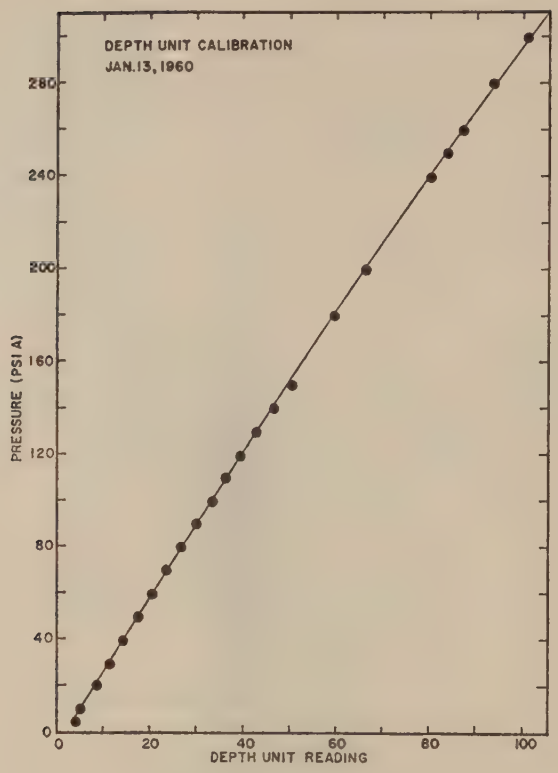

Figure 13. Depth unit calibration.

were taken, after which it was immersed in a water bath at 2–3°C for three hours before a second set of readings was taken. This procedure was repeated three times; the data are given in Table IV. The slight temperature effect observed should be taken into account if depth measurements are being made in arctic waters.

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Sverdrup, H. U., M. W. Johnson and R. H. Fleming
1942. The oceans. Prentice Hall, Inc., New York, 1087 pp.

TABLE III. Reproducibility of the Depth Unit (25°C).

Atmospheric Pressure			50 psia		100 psia		150 psia		200 psia		300 psia	
	Vibrotron Frequency	Unit Reading	Vibrotron Frequency	Unit Reading	Vibrotron Frequency	Unit Reading	Vibrotron Frequency	Unit Reading	Vibrotron Frequency	Unit Reading	Vibrotron Frequency	Unit Reading
	11107	0.0	10876	16.5	10660	32.5	10440	50.0	10214	66.0	09746	101.0
	11107	0.0	10876	16.5	10661	32.0	10440	50.0	10217	66.0	09746	100.5
	11107	0.0	10877	16.5	10661	32.0	10441	50.0	10214	66.5	09746	100.5
	11108	0.0	10876	16.0	10661	33.0	10440	50.0	10214	66.5	09746	101.0
	11106	0.0	10876	16.0	10661	32.0	10440	49.0	10214	65.0	09746	99.5
	11107	0.0	10876	16.5	10660	32.0	10440	49.5	10215	65.5	09746	100.0
	11107	0.0	10877	16.5	10661	32.5	10441	50.0	10215	66.0	09746	100.0
	11108	0.0	10876	16.5	10661	32.0	10440	49.5	10215	66.5	09746	100.0
	11106	0.0	10876	16.5	10662	32.0	10441	49.0	10214	65.0	09746	100.0
	11107	0.0	10876	16.5	10661	32.0	10441	49.5	10214	65.5	09746	100.0
	11107	0.0	10877	17.0	10662	32.5	10441	50.0	10215	66.0	09746	100.0
	11107	0.0	10877	16.5	10662	32.0	10440	49.5	10215	65.0	09746	100.0
Mean value	11107	0.0	10876	16.4	10661	32.2	10440	49.7	10215	65.8	09746	100.2
Standard deviation	0.6030	–	0.5222	0.257	0.454	0.335	0.522	0.390	0.904	0.582	–	0.451
Coefficient of variation (percent)	0.0054	–	0.0048	1.57	0.0063	1.04	0.00500	0.784	0.00885	0.885	–	0.450

TABLE IV. Temperature Effect on the Depth Element at Various Pressures*.

	18 January 1960			19 January 1960			19 January 1960	
	Room Temp.	Cold	Room Temp.	Room Temp.	Cold	Room Temp.	Cold	Room Temp.
Pressure*	25°C	2–3°C	25°C	21°C	2–3°C	25°C	2–3°C	25°C
psia	1300 PST	1530 PST	1645 PST	1022 PST	1155 PST	1335 PST	1605 PST	
0.....	0	0	0	0	0	0	0	0
50.....	15.5	15.0+	15.5	15.5	15.0+	15.0+	15.0	15.0
100.....	30.5	30.5	30.5	30.5	30.5	30.5	30.5	30.5
150.....	48.0 –	48.0 –	48.0 –	48.0 –	47.5	48.0	47.5	47.5
200.....	64.0	64.0 –	64.0+	64.5 –	64.0 –	64.0 –	63.5	63.0+
290.....	95.0	94.0+	95.0	95.0	94.0+	94.0+	94.0	94.0+

* The pressure gauge employed in this series was found to require recalibration, hence the pressure values given are not accurate.

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GROWTH AND REPRODUCTION OF THE OYSTER DRILL *EUPLEURA CAUDATA* IN THE YORK RIVER, VIRGINIA

By

Clyde L. MacKenzie, Jr.

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GROWTH AND REPRODUCTION OF THE OYSTER DRILL *EUPLEURA CAUDATA* IN THE YORK RIVER, VIRGINIA[1]

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Virginia Fisheries Laboratory, Gloucester Point, Virginia

INTRODUCTION

Eupleura caudata (Say) (Order Neogastropoda: Family Muricidae), the thick-lipped or rough oyster drill, is a close relative of the smooth drill, *Urosalpinx cinerea,* which occurs within the same geographical range along the shores of the Atlantic coast from Massachusetts to the eastern coast of Florida. Both species are well-known predators of oysters and perhaps other commercially valuable bivalves. Except in isolated locali-

[1] This research was conducted under a contract with the U. S. Fish and Wildlife Service, No. 14-19-008-2372, Study of Oyster Drills in Chesapeake Bay.

[2] Present address, U. S. Fish and Wildlife Service, Biological Laboratory, Milford, Connecticut.

ties, *U. cinerea* is the dominant species and as a result has received more scientific study. Until Haskin (1935) showed that *E. caudata* females deposit more embryos per case than *U. cinerea* in Barnegat Bay, New Jersey, and noted the differently-shaped cases, the only publicized difference between the 2 species lay in morphology of the shell. Though the species is present in some numbers on the bottom, McHugh (1956) did not find a single *E. caudata* among hundreds of drills collected from pier pilings in the vicinity of Gloucester Point, and we found only 3 in our samples of several hundred drills collected from pier pilings in this area. This indicates that the 2 species have different vertical distributions. Haskin (1935) and Galtsoff, Prytherch and Engle (1937) state that the species do not differ in their destructiveness of oysters. Stauber (1943) observed copulation by a single pair and he states that numbers of embryo cases deposited by caged females vary from year to year. Engle (1935) and Andrews (1955) briefly describe spawning patterns for a single year. Other than the fact that certain workers believe the ratio of *E. caudata* to *U. cinerea* is increasing in some localities, little is known about the natural history of this animal (Carriker 1955).

This study was undertaken to elucidate certain aspects of growth, reproduction, and ecology of *E. caudata* in the eelgrass zone of the York River, Virginia, to acquire basic information which might be used in controlling this pest.

This paper is part of a thesis submitted to the College of William and Mary in partial fulfillment of the requirements for the degree of Master of Arts. The writer wishes to express his deep appreciation to Dr. William J. Hargis, Jr. for suggesting the problem and for his valuable advice and criticism throughout this study. Thanks to Mr. Robert S. Bailey for taking the photographs, to Dr. J. L. McHugh for helping with the writing, and to many other people for their assistance. Drs. Jay D. Andrews and Melbourne R. Carriker, and Messrs. James B. Engle, John B. Glude, and W. A. VanEngel have generously given their time to reviewing the manuscript.

Materials and Methods

Description of the area

All drills studied were taken in the vicinity of the Virginia Fisheries Laboratory at Gloucester Point, Virginia, 6 miles from the mouth of the York River (Figure 1). This area is estuarine, salinities varying between 14 and 22 ‰ except during severe droughts and freshets. Oyster drills and several other snails live within the eelgrass *Zostera marina* zone, a strip about 50 yards wide in the experimental area bounded by Marshall's Pier and the ferry pier. The grass is dense and almost continuous. At extreme low tides the inner edge of the zone of grass is exposed and, because the bottom slopes moderately away from shore, the outer edge is rarely covered by more than 5 or 6 feet of water. The experimental area, behind the tip of Gloucester Point, does not have rapid currents. Wave action is usually light. Within this zone, *E. caudata* had a mean density of 3 per square yard; and *U. cinerea* had a mean density of 37 per square yard, as determined by careful examination of material removed from known areas of bottom. There is little likelihood that drills migrated into or out of the experimental area because drill traps (see discussion below) placed under piers on either side or offshore of it where there was no eelgrass collected virtually no drills. Several samples of embryo cases were obtained at Tillage's oyster ground located upriver from the laboratory (Fig. 1). Except where noted, samples were taken from the experimental area.

Aquaria

Running-water aquaria of approximately 2.7 ft^3 capacity were employed to make close observations of copulation. River water from the end of the laboratory pier was continuously supplied through lead pipes by centrifugal pumps.

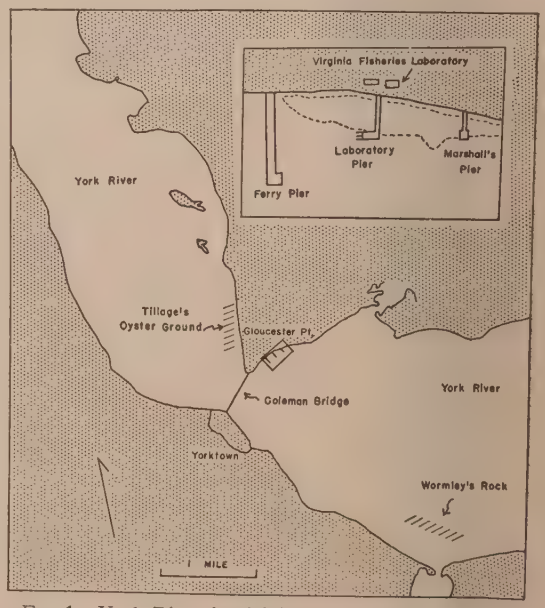

Fig. 1. York River in vicinity of the Virginia Fisheries Laboratory showing collecting sites. Inset shows experimental area. Dashed line shows extent of eelgrass.

Cages

Several phases of this study were conducted in cages, suspended along the laboratory pier one foot above bottom with about one to 3 feet of water covering them (Figures 2 and 3). Cages consisted of wooden frames with masonite bottoms. The sides and removable top were covered with large-mesh plastic screen, 4 holes per linear inch. Masonite dividers prevented contact between drills in adjacent compartments.

FIG. 2. Experimental cage with its screen bottom and compartments.

FIG. 3. Experimental cage, oyster tray, and davit used to raise and lower cage.

The cages, 37 inches long, 16 inches wide, and 6 inches deep, contained from 2 to 12 compartments each. Later models incorporated plastic screen bottoms (8 holes/inch) which permitted sediments to pass through. For support and stability, cages were placed in seasoned, tarred oyster trays similar to those used by Hewatt and Andrews (1955). Except where noted, several one- and two-year-old oysters were placed in each compartment as food and were not replaced the whole summer unless they were completely consumed by drills.

Traps

Drills and many embryo cases were obtained with traps consisting of flat, 27 × 12 inch chicken-wire bags containing small oysters and often barnacles and mussels as bait. To minimize tipping of traps upon lifting, which tends to shake out drills, traps were tied in the center of the flat side by a rope attached to a small buoy. Drills that moved to the bait were collected by carefully lifting the traps and shaking them into a shallow screen tray. Since there was a possibility that they reduced the abundance of drills locally, traps were moved to new areas after each collection to secure as many drills as possible.

Temperature

Temperature records were compiled from data collected at the U. S. Coast and Geodetic Survey tide station located at the end of the laboratory pier. Since cages and traps were 5 or more yards inshore of the temperature recorder and in shallower water, temperatures at cage and trap sites may have been slightly different from those at the tide station.

Determination of sex

The method developed by Hargis (1957) to determine sex of living snails was used. He found that oyster drills held under water would attach to one's finger. By carefully rolling the shell back the presence or absence of a penis can be detected.

Measurements

Measurements of drills made with vernier calipers and cited in millimeters are of the long axis of the shell from apical tip to siphonal tip, usually termed shell height. Cases and embryos were measured microscopically using a calibrated ocular micrometer.

GROWTH

Pattern of growth

After the initial varix (raised ridge on outside surface of univalve shell parallel to the lip) has formed when the drill is 10 to 15 mm in height,

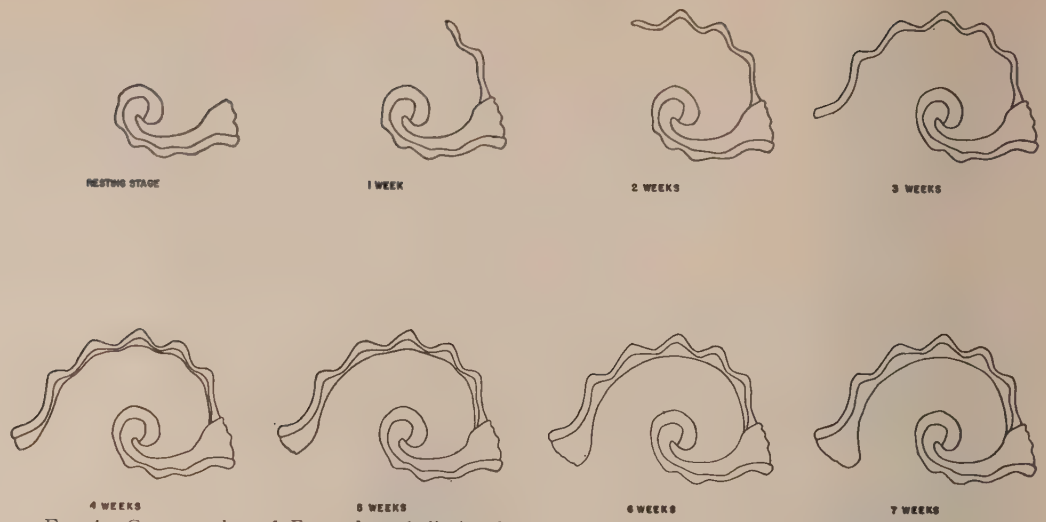

FIG. 4. Cross section of *E. caudata* shell showing pattern and approximate rate of growth. Some drills produce a flange of shell at each axial rib, not like rounded ribs as those in figure. Weeks 1-3 are termed thin-lip stages; weeks 4-7, thick-lip stages.

shell growth in *E. caudata* usually occurs as a thin layer which begins at the inner edge of the varix and without stopping to reinforce proceeds through an arc of 180°. After flaring out to form the next varix, the animal then reinforces this thin shell by depositing successive layers of shell on the inside (Figure 4). Thus thin lips are usually an indication of active growth. With the formation of each half whorl of new shell, a growth ridge, a line of demarcation between the old siphonal canal tip and the new shell, appears on the siphonal canal, and the old mark is grown over (Figure 5). During winter the thin shell covering the tip of siphonal canals of mature drills is often broken or eroded. During summer drills deposit enough new shell to cover the siphon but, unless accompanied by lateral growth, this is merely repair of shell damage and not actual growth. Moore (1936) and Hancock (1959) have shown that *Purpura lapillus* (= *Thais lapillus*) and U. *cinerea,* respectively, both prosobranch muricids, also produce a thin layer of shell which they subsequently reinforce.

Most drills from the experimental area showed a light yellowish outer layer and purplish reinforcing layers. In *E. caudata etterae* B. B. Baker (the large ecological form of *E. caudata*) from Chincoteague Bay, Virginia, however, both layers were light.

FIG. 5. Shell of *E. caudata* showing its conspicuous siphonal growth ridge.

Interpretation of the growth mark

Growth ridges or rings in many bivalves have been shown to be deposited once a year. No attempt will be made here to review all the species studied, but growth rings are year marks in the Pismo clam (Weymouth 1923), in the Pacific

razor clam (Weymouth, McMillin and Holmes 1925), and in the Pacific cockle (Weymouth and Thompson 1931). To the writer's knowledge only Magalhaes (1948), who found that from none to 3 growth ridges a year with no apparent relationship to age are deposited on shells of *Busycon canaliculatum* and *B. carica,* and Clarke (1956), who without experimental evidence states that ridges on shells of *Nassarius trivittatus* are probably useless for determining age, have treated this subject with reference to snails. Cole (1942) assumed that siphonal canal ridges in British *U. cinerea* represent yearly markings and attempted to use them to determine age of drills. Andrews (1956), however, has questioned the validity of these ridges in *U. cinerea* as year marks.

The distance from growth ridges to the siphonal tip in *E. caudata* may range from 2 to 6 mm. If a year class (see below, *Recognition of year classes*) of drills large enough to have growth ridges grew more than this during a summer, many individuals would show more than one half whorl and coincident varices and growth ridges.

In May, 1956, drills with a varix ranging in height from 12.8 to 26.2 mm were caged and measured individually once a month until fall, 1957, through 2 summers and a winter. Since growth of *E. caudata* ceases at sexual maturity (see below), mature drills did not grow either summer. It was discovered that growing drills did not deposit a consistent number of half whorls. Eight of them each deposited 2 half whorls in one summer. This amount of growth appears to be normal because many drills collected in the experimental area showed 2 half whorls of shell that looked new, and several marked drills in other cage experiments deposited 2 half whorls in a summer. Seventeen drills deposited one whorl in a summer, but only 2 of these showed growth in both summers. Thus, varices and siphonal canal growth ridges in this species cannot be considered as yearly markings and appear to have little value for aging. They are merely growth stoppage marks.

Rate of shell growth

Rate of deposition of half whorls and reinforcement of them were estimated by examination of caged drills at 2-week intervals. Half whorls were deposited in 3 weeks, on the average, and reinforced in 4 weeks (Figure 4). Because the amount of food was not carefully controlled, these rates should be considered approximate. Food in the form of seed oysters was always available to drills, but their number and size, particularly, were not kept constant.

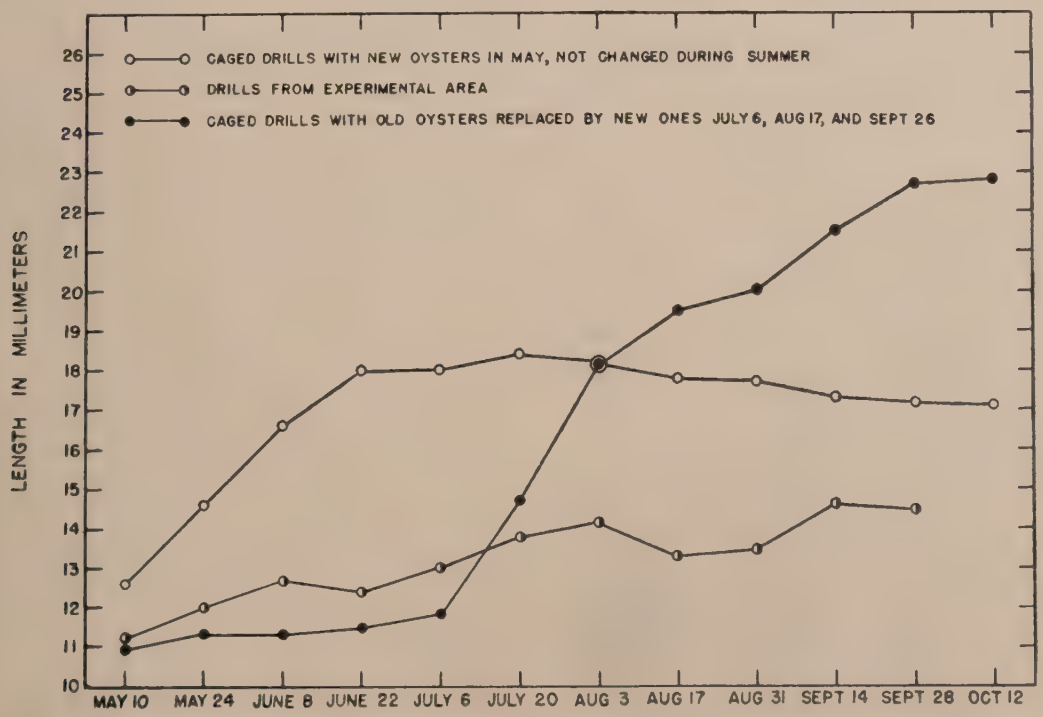

FIG. 6. Growth rates of age-group I *E. caudata* with three different food situations, summer 1957.

Growth on different amounts of food

To determine whether amount of food influences rate of growth, 3 lots of *E. caudata* of age-group I, each feeding on different amounts of food, were compared in 1957 (Figure 6). In the first lot, 64 drills were caged together on May 10 with old oysters which the drills did not bore. By July 20, all but 28 drills were dead and growth from May 10 to July 6 was negligible. On July 6, August 17, and September 26, new seed oysters encrusted with barnacles and mussels were placed in the cage. After July 6, growth was immediate and rapid and no more drills died after July 20. The 28 remaining had doubled their length by the end of September.

In the 2nd lot a pair of drills was placed in each of 12 compartments of a cage, which contained a cluster of new seed oysters with barnacles and mussels which were not changed during the entire summer. Growth was rapid until June 22 when the original heights had increased by almost one half. After this date, probably because the desirable foods had been consumed, growth ceased for the rest of the summer. Average heights actually diminished by erosion of the siphonal tip by handling.

In the 3rd lot, mean heights of drills of age-group I collected from the experimental area were determined each 2 weeks. Growth was slow as mean heights of drills increased from 11.3 to just 14.5 mm from May to the end of September.

These results suggest that amount of food has great influence on rate of growth of *E. caudata,* and that food supply is an important consideration in experimental work. With ample food, drills appear to grow much faster than they do in nature.

Cessation of growth at sexual maturity

Moore (1936, 1938) stated that *T. lapillus* ceases growth at sexual maturity. If onset of maturity in females is defined as the time when they are capable of depositing their first embryo cases and in males as the functional ability to copulate, the following data indicate a similar pattern of growth for *E. caudata.*

Beginning on June 25, 1957, a record was kept of numbers of drills in trap catches which showed evidence of recent growth, *i.e.* thin marginal lips. Though 185 of 1,108 (16.7%) age-group I drills showed thin lips, only 2 of 522 (0.4%) age-group II+ drills showed them.

In 1956 only one of 10 caged females which deposited embryo cases showed evidence of growth and that individual deposited only a half whorl of new shell. Of the 10, eight survived the winter and none grew in 1957. Of 17 other females isolated in 1956, twelve deposited cases for the first time in 1957, and did not grow during the summer. Three of the 5 reproductively-inactive in 1957 showed no growth, while one grew 2 half whorls and the other, one half whorl. It thus appears that females show little or no shell growth after embryo case deposition begins.

In 1956 only 10 of 30 caged males (height range 14.4 to 23.3 mm) grew; one of these grew 2 half whorls and 9 grew one half whorl. Since the heights range of the 30 matches that of mature copulating males, presumably most of these males were mature (Table I). Of 24 of the same males carried through 1957, 22 showed no growth and 2 grew a half whorl.

TABLE I. Height frequencies of copulating drills

Total height (mm)	Pairs in Aquaria 1956		Pairs in Cages 1956		Pairs and Trios in Cages 1957	
	♀	♂	♀	♂	♀	♂
14.5	—	1	—	—	—	—
15.5	—	1	—	—	—	—
16.5	1	2	—	1	—	1
17.5	0	5	—	5	—	5
18.5	0	4	—	10	—	8
19.5	2	3		2	—	10
20.5	1	0	6	11	—	6
21.5	3	3	6	10	1	4
22.5	6	7	7	5	3	1
23.5	2	2	10	—	20	6
24.5	4	—	12	—	5	1
25.5	1	—	2	—	5	—
26.5	3	—	1	—	3	—
27.5	2	—	—	—	2	—
28.5	2	—	—		—	—
29.5	1	—	—		—	—
30.5	1	—	—	—	—	—

Another indication that growth ceases when drills reach maturity is that the right limb of the height-frequency-distribution curve representing age-group II+ does not shift to the right through the growing season (Figure 7).

Recognition of year classes

Estimation of age by height frequencies

From July to November 1956 and from May to October 1957, heights of drills taken in monthly trap catches were recorded, grouped into one-mm intervals, and plotted as percentage frequency polygons (Fig. 7). In July 1956, height frequencies showed what appeared to be a single modal group. This mode showed a definite progression to the right with each successive month of 1956, and is clearly represented as the large portion of the right-hand modal group each month in 1957.

In late August 1956, five small drills appeared in trap catches and a few more were collected in

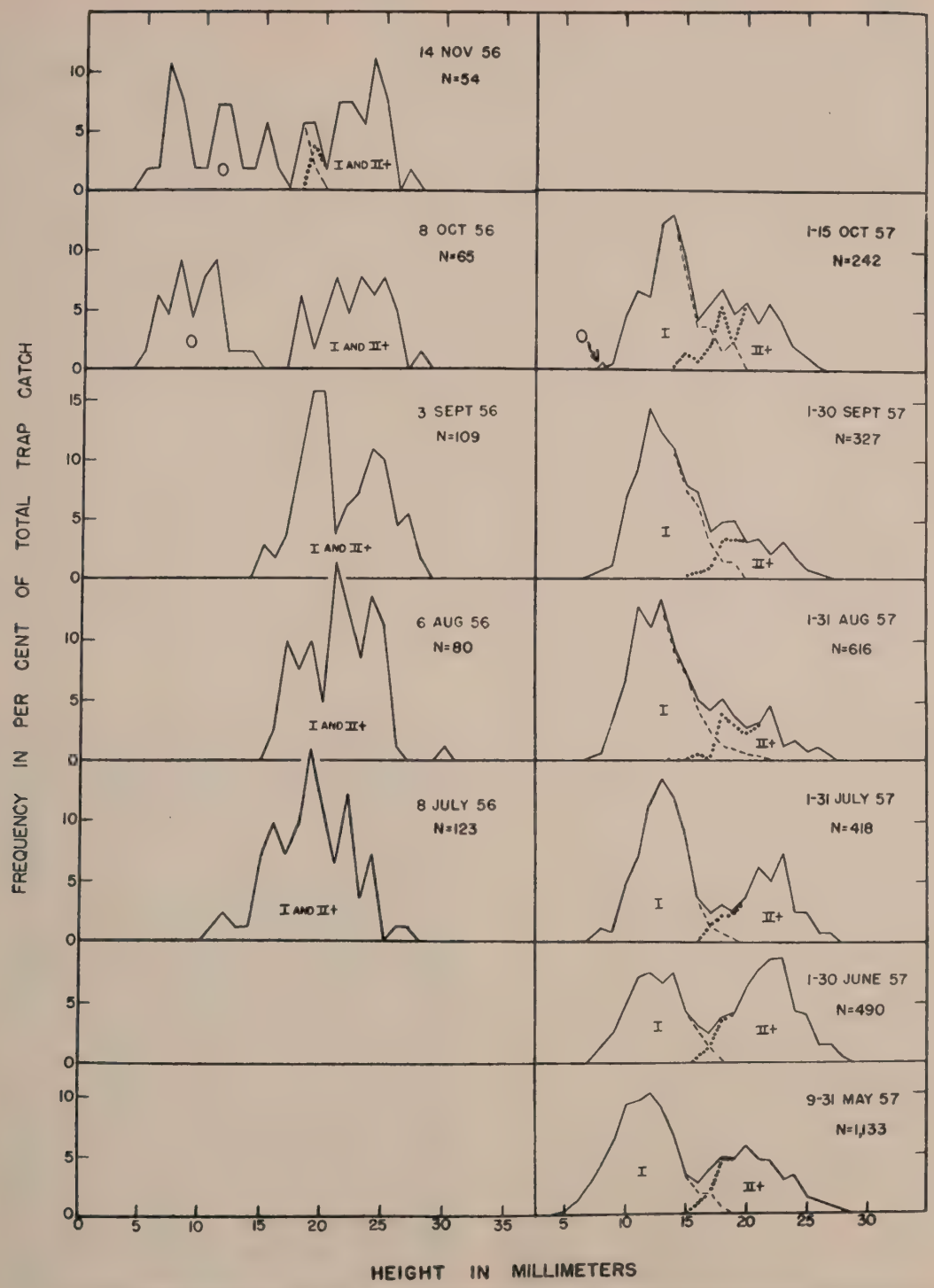

FIG. 7. Monthly trap catches of *E. caudata* in experimental area showing height frequencies of age groups O, I and II+. (The plus sign indicates age-group II and older).

September. Of 43 collected in October, a random group of 32 was measured and plotted along with the rest of the catch. This modal group with a range of 5 to 14 mm was separated by more than 3 mm from older drills. In the November 1956 sample, and in monthly samples of 1957, the left mode corresponds with the left mode of the October 1956 sample.

It is probable that drills in the left modal group in the October 1956 sample belong to age-group O. There are only 5 mm to the left of it in which to include a younger age group and separate the 2 groups by more than 3 mm. It would be unusual for age-group O to be less widely separated from the I's than the I's are from the II+'s. When first collected in late August, these drills were quite large, but in earlier observations of *U. cinerea* by Dr. J. L. McHugh (personal communication), suspected young-of-the-year drills had reached a mean size of 6 to 8 mm when they were first collected in August and September. Apparently young-of-the-year drills are not available to traps until mid-summer. Growth rate of age-group O *E. caudata* on natural bottom is unknown, but conceivably may equal or exceed that of older drills which grew from 12 or 15 mm to over 20 mm in 4 or 5 months in cages. Most *E. caudata* conchs emerged from cases during the first week of July at a height of 0.9 mm. Thus, in 3 months they had grown 5 to 10 mm.

The right modal group of the October 1956 sample probably represents age-group I and older drills. *E. caudata* ceases growth at maturity and, therefore, modal height groups coalesce. Growth of age-group I drills in 1957, as indicated by progression of the modal group about 3 mm to the right, is believed slower than in the previous year because lower height limits of the early 1956 samples were much farther to the right than those of the 1957 samples. In 1957, drills of age-group I grew much faster in cages than on natural bottom (Fig. 6). Slow growth on natural bottom may have been the result of intensive competition following a large spawning in 1956 and subsequent overcrowding of the environment. It is striking that age-group I drills are dominant in the catch in 1957. Such dominance of a year class, if it does lead to intensive competition, may subsequently affect other phases of the drill's life history, such as size of succeeding broods and age at sexual maturity.

In 1957, on October 3, only one recognizable individual (8.0 mm) of age-group O was taken. This apparent lack of young-of-the-year drills may have been the result of limited spawning and hand removal of a large percentage of the embryo cases from the experimental area.

Hancock (1959), in England, found that sizes of laboratory raised *U. cinerea* of known age fell within modal size groups of drills from nature which, because of their size relative to other drills and time of appearance in collections were suspected to be of a particular age.

Estimation of age by shell characters

Since large old-appearing shells are well-worn, it is apparent that shells of *E. caudata* erode gradually. From this, it was decided to test the hypothesis that drills could be sorted into age groups on the basis of the degree of shell erosion. *E. caudata* is perhaps an ideal gastropod to be aged by this method because the young hatch out in a period lasting only about 7 weeks, hence distinct differences in degree of shell erosion between age groups might be expected. Presumed age-group O drills of the October 1956 sample were smaller than those caught in earlier catches, and also differed in that the protoconch shell was entire and the axial and transverse ribs were sharply sculptured and not noticeably eroded. Part, or sometimes all, of the protoconch shell eroded away during the winter of 1956-57, but these drills, now called age-group I, could still be separated from older *E. caudata* because the sharp apex of the spire and the sharply-chiseled appearance of the shell sculpture had not appreciably changed. Older

Fig. 8. Drills of age-groups O, I and II+. Axial ribs noticeable on second whorl (first whorl is apical whorl) in O specimen, on third whorl in I specimen, and on fourth whorl in II+ specimen.

TABLE II. Accuracy of observers in separating age groups, using defined morphological characteristics

Observer	Age Group I					Age Group II+		
	Original number	Agreement	Disagreement*	Uncertain	% Agreement	Original number	Agreement	% Agreement
A	109	109	0	0	100	32	32	100
B	109	108	1	0	99.1	32	32	100
C	109	108	1	0	99.1	32	32	100
D	108	106	0	2	98.2	32	32	100
E	108	108	0	0	100	32	32	100

* Called age-group II+.

drills, labeled age-group II+, had blunt spires and smooth ribs.

A summary of characters used to separate age-groups I and II+ on August 23, 1957, and age-group O on October 3, 1957, (Figure 8) follows:

Age-group O—Apex of spire sharp, protoconch shell entire, no noticeable erosion of shell, size small;

Age-group I—Apex of spire sharp, remnant of protoconch shell usually present, apical whorl less than 1 mm in width, axial ribs usually sharply sculptured, size moderate;

Age-group II+—Apex of spire blunt, apical whorl 1 mm or greater in width, axial ribs blunt or sharp only on last half whorl, size large.

To test reproducibility of these shell characters several laboratory staff members were asked to separate a mixed sample of age-groups I and II+. The sample had been sorted previously into groups and ages marked by inserting labeled pieces of paper into the shell cavities. Characters used to separate the groups were carefully described to the experimenters, and sample drills were furnished. In each test, drills were sorted with almost 100% agreement (Table II).

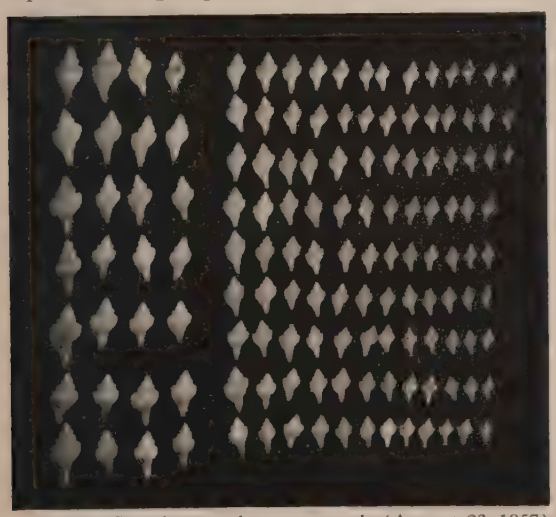

FIG. 9. Complete random trap catch (August 23, 1957) of *E. caudata* sorted by shell characters into age groups, II+ on left and I on right.

Figure 9 shows the complete catch of August 23, 1957, grouped by shell characters into age-groups I and II+.

Ages determined from height-frequency distributions and shell characters

When *E. caudata* in October and November 1956 trap catches were separated by shell characters, the height-frequency distributions of age-group O drills corresponded almost exactly with the left-hand modal group in the height-frequency polygon, and combined age-groups I and II+ drills corresponded with the right-hand modal group. In all 1957 samples, correspondence was equally close.

In May and June of 1958, these same year classes, now age-groups II and III+, could still be distinguished from each other on the basis of both height-frequency distributions and shell characters. No recognizable age-group I drills were seen.

Although much of this evidence is circumstantial and does not absolutely establish ages of individuals, shell characters are probably reliable indicators of age for most drills in a sample.

To determine age in other areas where rate of shell erosion probably differs, it may be necessary to identify the current year class late in summer and then follow it and succeeding year classes for several years. Rate of erosion could be determined by preserving shells obtained by regular sampling of a particular year class. The samples could be compared with drills of unknown age. I feel that year classes can be identified on the basis of shell characters alone after growth stops at sexual maturity when age cannot be estimated on the basis of height.

REPRODUCTION

Age and height at sexual maturity

I early suspected that female drills did not mature until after their 2nd summer of life, because

in 1956, of 30 females in cages, only 11 large ones deposited embryo cases. Young-of-the-year were not yet hatched when the drills were caged, thus many of the 19 remaining were undoubtedly in their 2nd summer or age-group I. Sixteen of the 19 non-spawning females in cages survived the winter of 1956-57 and 10 deposited embryo cases in 1957. In another experiment, 9 pairs of age-group I drills (range 7.1-17.8 mm) were isolated in separate compartments of a cage for the entire summer of 1957. Since most drills were insufficiently developed to be sexed when the experiment was begun, some pairs may have been of mixed sex. Also, mature males (heights 23.1 and 23.2 mm) were paired with 2 age-group I females (14.1 and 17.1 mm) in this cage. No embryo cases were deposited by any age-group I females in these tests though many were deposited by older caged drills. In addition, females less than 19 mm were never observed depositing embryo cases.

It was not determined what proportion of females is mature during the spawning season of their 3rd summer of life.

Tables I and III show the extensive range of heights of mature females. Since there is good evidence that females cease growth at sexual maturity, this suggests considerable individual variation in growth or age at maturity. The minimum height of mature *E. caudata* in the experimental area appears to be about 19 mm for females and 16 mm for males. Preliminary data obtained from examination of the gonads of large numbers of drills show that males mature at a younger age than females.

Sex ratio

Sex ratios were obtained by examining drills collected on traps. Age groups were not recognized in 1956; hence, sex ratios of different year classes could not be determined. Ignoring age differences, the July, August and September samples show a nearly 50:50 ratio, but samples in the 2 succeeding months contained significantly more females (Table IV). In 1957, considering age-group II+ only, males were slightly in predominance in May, but beginning in June in each month until September a larger proportion of females came to the traps (Table V).

TABLE III. Sizes of females which deposited embryo cases in cages or on traps

Total height (mm)	No. of Individuals	
	1956	1957
19.5	3	1
20.5	3	3
21.5	7	4
22.5	10	0
23.5	12	7
24.5	12	5
25.5	8	6
26.5	3	6
27.5	1	2
28.5	0	3
29.5	0	0
30.5	0	0
31.5	1	0
32.5	0	1
Total	60	38

TABLE IV. Sex ratios of 1956 trap samples (Age-group O not included)

Date	Uncertain	♀♀	♂♂	Total	% ♀♀
July 8	8	38	37	75	50.6
Aug. 6	7	34	41	75	45.3
Sept. 3	4	58	46	104	55.8
Oct. 8	0	25	10	35	71.4
Nov. 14	0	24	6	30	80.0

TABLE V. Sex ratios of 1957 trap samples (Age-group II+ only)

Date	Uncertain	♀♀	♂♂	Total	% ♀♀
May 8	1	25	39	64	39.0
May 11	0	9	27	36	25.0
May 13	0	15	29	44	34.6
May 15	0	20	23	43	46.5
May 22	0	31	33	64	48.4
June 5	0	21	18	39	53.8
June 18	0	46	29	75	61.3
July 4	1	31	19	50	62.0
July 17	0	15	6	21	71.4
July 31	0	30	9	39	76.9
Aug. 20	0	5	0	5	100.0
Sept. 4	0	7	6	13	53.8
Sept. 26	0	5	4	9	55.5
Oct. 9	0	11	13	24	45.8
Oct. 25	0	4	0	4	100.0

The percentages of females occurring on the traps appeared to follow the seasonal cycles of copulation and spawning (Figures 10C and 11C). It is possible that the sexes move to shells or traps in about equal numbers, copulate, and when copulatory activity wanes and spawning begins, larger and larger numbers of females move to shells in traps which provide sites for their embryo cases free from siltation. Females apparently have a greater tendency than males to move to shells projecting above the bottom, particularly during the spawning season, and this results in selective sampling by traps. Samples taken after July 31 are probably too small to be significant but nearly equal numbers of each sex in the October 9 sample may be a result of the fall copulating period. Unfortunately, many age-group I drills could not be sexed in 1957 because they were too immature, thus sex ratios were not determined.

In English waters, both Cole (1942) and Hancock (1959) found sex ratios of *U. cinerea* unbalanced in favor of females during the spawning season.

Evidence against sex reversal

Nineteen females and 21 males isolated on May 16, 1956 survived to August 31, 1957, sixteen months later, and retained their sexual identities. Eight other females and 7 males, isolated for periods of 3 to 14 months, had not changed sex at the end of the period.

Examination of external reproductive organs of drills and smears of gonads of over eight-hundred males and females gave no evidence of actual or potential hermaphroditism. Mature females possess yellow, white or orange gonads with large lobes containing vitelline bodies. Mature males possess large penes, yellow or orange gonads with small lobes containing spermatozoa, and usually swollen vasa deferentia. Neither contained organs or parts of organs typical of the opposite sex.

Copulation and overwintering of spermatozoa

To copulate, the male usually assumes a position on the lower right side of the female with his siphonal canal pointing in the same direction as hers (Hargis and MacKenzie, in press). His foot, after extending to the rim of the mantle cavity of the female, forms a groove in its anterior end through which the penis is inserted through the mantle cavity and into the vagina. Actual copulation lasted as long as 4 hours and 39 minutes. Most pairs copulated, ceased for a few hours, and then resumed intermittently for 24 to 48 hours. Promiscuity appears to be a natural phenomenon because drills in aquaria and cages copulated repeatedly with various partners. Hancock (1959) indicates that *U. cinerea* is polygamous. Often a trio of *E. caudata,* 2 males copulating with one female at the same time, was seen. Figure 10 B and C shows that copulation begins early in April and ends early in July, but occurs again through October. In cages copulation was much less intense in 1957 than in 1956.

Females collected from the experimental area and cages in late fall deposited cases with viable embryos the next spring, and thus these drills appear to retain spermatozoa for at least 6 months.

Seasonal activity

Little is known of the seasonal activity of individual gastropods. To study this aspect of their

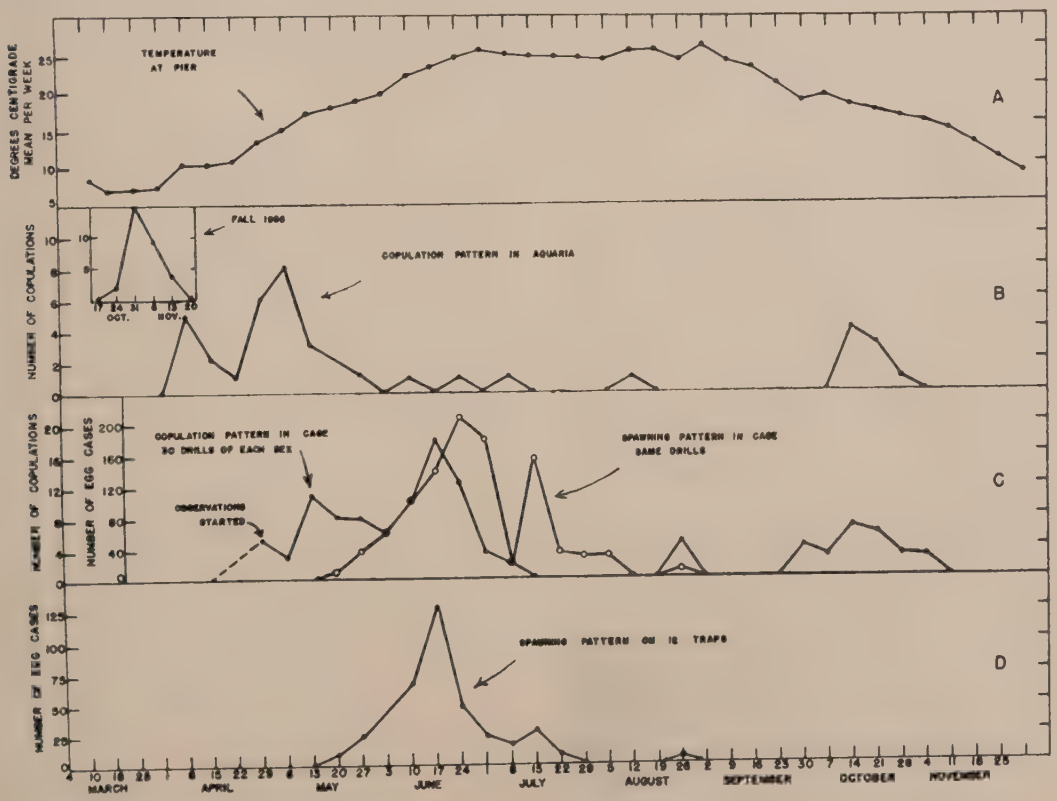

FIG. 10. Seasonal patterns, grouped by weeks, of temperature, copulation, and spawning in 1956.

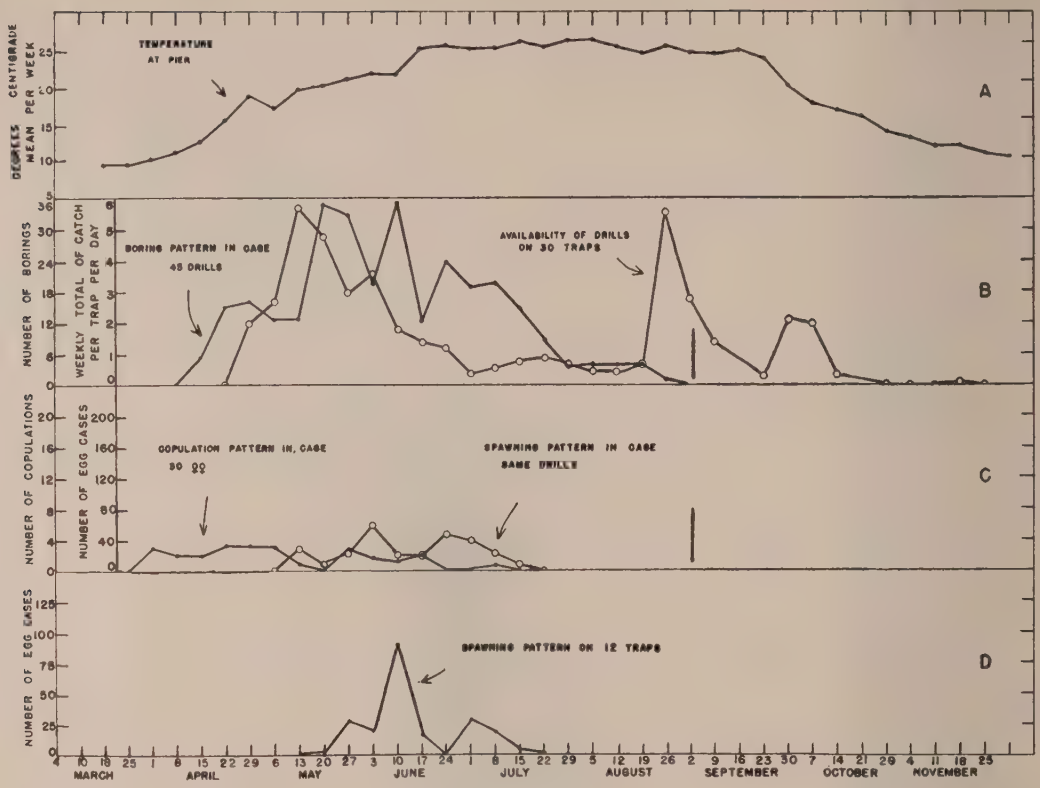

FIG. 11. Seasonal patterns, grouped by weeks, of temperature, boring, trap catches, copulation, and spawning in 1957. Solid vertical bars indicate termination of observations.

behavior, 45 *E. caudata* individually marked with a fast drying paint on March 2, 1957 were placed in a cage which was lifted at 2-day intervals to record copulation, deposition of embryo cases and drilling. A pair in copulatory position was recorded as copulating if the male's penis or copulatory groove could be observed; drilling was recorded if the snail was located over a freshly bored hole; positive identification of spawning was often uncertain, but a female seen amidst a cluster of new cases in the normal case laying position was considered the one which deposited them. The cage was examined 75 times from April 4 to September 6.

Figure 11C shows that copulation, which began 2 weeks before boring, was the earliest recorded activity. Later, copulatory activity of both sexes was interspersed with feeding. Only 3 females were observed depositing embryo cases during this period. Reduced spawning in cages corresponded to reduced spawning in natural populations during the same period. One female may have copulated after depositing embryo cases. Over half the females were not observed copulating during the period and several drills were not seen boring. On the average, females were found drilling 7 times during the 75 observations, but males only about 3 times. Drilling and feeding normally persists for several hours or days, and it is likely that most of this activity was seen and probable that these differences are normal. Actual copulation, which lasts at most only a few hours, was undoubtedly missed in most individuals.

In 1957, traps with new seed oysters from the James River were placed in the experimental area in late March and records of their catches were kept the entire summer. Catches were negligible until the week of April 29 when the mean weekly water temperature rose from 15.8°C to 19.2°C (Fig. 11B), then increased steadily to the week of May 13 (20°C), thereafter declined steadily to July 1, and only small numbers of drills came to traps until August 26. Most traps were then rebaited, and large catches were recorded again. Several traps were left with the original oysters, and the catches remained very low although they did increase slightly. Data collected by Dr. J. L. McHugh show that catches of *U. cinerea* on traps, baited with oysters not changed during summer, were smaller in July and August than in spring

and fall. This pattern seems to support the work of Janowitz (1957) who found that drills are more attracted to growing oysters. McHugh (personal communication) states that maximum oyster growth at Gloucester Point occurs in spring and fall. Soon after rebaiting traps, catches diminished quickly as the smallest seed, barnacles, and mussels were consumed. The catch of September 23 was about equal to the low catches of July 1 through August 19. Traps were rebaited again on September 26, but succeeding catches were less than half those of August 26, undoubtedly because of decreased activity caused by lower water temperatures. Again the catch dropped off quickly and drills were scarce after the week of October 7 as water temperatures dropped below 17.8°C. Clearly these observations support those of Stauber (1943) and McHugh (1957) who also report that rebaited traps catch more drills. These catch records and cage observations show that this species is active only for about 6 or 6½ months a year. Andrews (1956) found that *E. caudata* came on traps only for about 6 months at Wormley's Rock in the York River.

Drilling observations in the cage were compared with weekly trap catches (Fig. 11B). Caged animals commenced boring at a temperature of 12.5°C, about 2 weeks before drills came on traps; thereafter, boring activity in cages lagged a week or more behind similar activity in nature. Boring and catch intensities paralleled each other roughly, however, and both diminished to a low point during the first part of August. Since large catches were obtained the week of August 26, after traps had been rebaited, drills presumably were still partially active; probably decreasing catches and reduced frequency of boring in July and early August largely mirror decreasing attractiveness of bait rather than inactivity or aestivation. No experiments were conducted, however, to determine whether general activity decreases during mid-summer.

Spawning period

Spawning periods of drills were studied by Engle (1935) in Delaware Bay and Andrews (1956) in the York River. Both recorded the numbers of *E. caudata* and *U. cinerea* embryo cases in drill traps. In Delaware Bay cases were deposited during the period May 23 to July 25, with greatest numbers during the week of June 13. Perhaps because his sample was smaller (110 cases), Andrews (1956) found the duration of spawning even shorter, June 13 to July 18. These workers found that the spawning period of *U. cinerea* begins earlier in spring and extends later into summer than that of *E. caudata*. Other studies on *U. cinerea* have reported a 2nd smaller spawning in some summers with a peak usually in September (Galtsoff *et al.* 1937, Cole 1942, Stauber 1943).

Embryo cases at Gloucester Point were collected in traps and a cage. During 1956, 12 traps were examined between the laboratory and ferry piers. Spawning began on traps and in the cage about May 20 at a temperature of 18.3°C (Fig. 10C and D), reached a peak during the week of June 17 when the mean temperature was 25.5°C, and ceased late in July. In the cage the peak occurred about one week later and spawning ceased in early August. A small flurry of spawning on August 26 as shown in figure 10C may have been stimulated by the slight decrease in temperature.

In 1957, 15 traps were set out in each half of the experimental area. Spawning began in the cage on May 13 at 20.0°C and on traps about May 20 at 20.6°C (Fig. 11C and D). There was no distinct peak in the cage and spawning was much less intense than in 1956. Seventy-eight cases were deposited when the traps were placed in a new section of the experimental area for 3½ days during the week of June 12. This one record for a half-weekly period is twice as high as that of any other full week and therefore may be abnormal. Hargis (personal communication) reports that numbers of embryo cases of *E. caudata* in comparable eelgrass areas were negligible in 1957 as compared to 1956. The effects of decreased spawning in 1957 became apparent when no identifiable drills of age-group O were collected on traps until October 3. In marked contrast, many small drills had already been collected by late August and September in 1956.

These spawning periods agree with those observed by Engle in Delaware Bay but are more extensive than those recorded by Andrews. There was no late wave of spawning of *E. caudata* embryo cases as reported for *U. cinerea*.

Embryo case deposition may be interrupted or inhibited by the frequent examination of traps or by unsuitable oysters within traps resulting in low numbers of cases. As an example, only 5 clusters (49 cases) were obtained from 15 traps in the down river half of the experimental area in 1957; whereas on shells, a few hundred cases were collected from that area. New cases were also collected on shells after spawning ceased on traps.

Intensity and duration of embryo case production

Previous studies of intensity and duration of embryo case production in *U. cinerea* are of limited value because the actual numbers of females under observation were not known (Carriker 1955). Various authors have estimated that *U. cinerea* females deposit about 25 to 50 cases a

spawning season. Nelson (1922), Engle (1940), Cole (1942), and Hancock (1959) state that *U. cinerea* do not deposit all their cases at one time, but may lay several clusters in a spawning season.

Because nothing was known of this phase of reproductive activity for *E. caudata,* experiments were designed to determine the numbers of cases deposited by individual females of various heights. Pairs of females and males graded from the smallest to the largest available were put into compartments of 3 cages on May 16 before spawning had begun. The compartments of a 4th cage housed pairs each about 20 mm in height. Several one- and 2-year-old oysters were placed in each compartment. Cages were cleaned weekly when embryo cases were counted. The experiment was continued in 1957 with the same animals, but with new oysters which were not changed during the summer unless they were completely consumed. Missing or dead animals were replaced by May 11, 1957. The cages were examined and cleaned periodically during the winter.

TABLE VI. Duration and intensity of spawning by individual caged females

Year	Initial Height (mm)	Duration (weeks)	Number of weeks inactive	Total embryo cases
1956	19.4	8	2	63
	20.7	8	1	61
	21.1	7	0	95
	22.0	1 cluster**	0	2
	23.3	8	1	46
	24.0	4	1	17
	24.1	10	3	45
	25.7	5	0	37 or 38
	26.7	6	1	25 or 26
	27.8	2	0	29
	29.0	8	1	95
		—		
		6		
1957	19.7	7	2	54
	20.0	3	1	15
	21.7	11	0	174
	23.0	4	1	37*
	23.0	5	0	49
	23.7	4	0	64
	23.7	1 cluster**	0	9
	23.8	6	2	71
	24.3	10	4	71
	24.4	8	3	45
	24.7	6	0	68
	24.8	8	2	79
	25.2	2	0	14
	25.3	3	0	22
	25.4	9	1	114
	25.7	7	2	28
	26.0	1 cluster**	0	3
	26.0	8	1	76
	26.3	7	3	60
	27.6	12	4	107
	32.3	4	0	57
		—		—
		6		55 (1956 & 1957)

* Lost June 8 and excluded from mean.
** Called duration one week.

Number of embryo cases

The mean number of embryo cases per season per female was 55 (range 2 to 174, Table VI). Apparent differences in embryo case production in the 2 years may not actually mirror conditions in the experimental area for differences may have been caused by factors such as kinds and amounts of food which were not carefully controlled (Table VII). Also, it is not known if fertility of males changes with time.

TABLE VII. Comparison of the total number of cases deposited by the same females in successive years

Serial number of drill	1956	1957
1	61	54
2	63	45
3	95	15
4	29	60
5	25 or 26	22
6	46	9
7	45	71
Mean	52	39

Females retained from 1956 and reproductively active for the first time in 1957 laid an average of 77 cases. Two females that deposited cases in 1956 did not do so in 1957.

The number of cases females in the experimental area deposit was not determined. However, sizes of clusters found on the bottom were about the same as those deposited by caged females (Table VIII). One hundred and thirty-six clusters containing about 10 cases each were deposited by 23 caged females in 1957. The mean number of embryo cases contained in 232 clusters from shells collected randomly in the experimental area was about 9. Observations of particular compartments over a period of a few weeks showed that females deposited small clusters of cases, desisted for a short period and later resumed this activity.

TABLE VIII. Comparison of numbers of cases per cluster on shells in the experimental area with those deposited by caged females, summer 1957

No. of cases per cluster	Cages hauled each week	Natural bottom	Cage hauled every two days*
1-5	31	31	49
6-10	44	80	26
11-15	49	51	8
16-20	8	18	2
21-38	5	6	0
Totals	136	232	85

* Not compared in text with other two distributions.

Females deposited an average of 6 clusters (range one to 18).

The number of cases deposited by a female is apparently independent of her size. Of 31 females that deposited cases in captivity the smallest 14 laid an average of 58.2 cases, the largest 17 an average of 51.5. The difference is not statistically significant, ($\chi^2 = 0.03$, d.f. $= 1$, $P = 0.86$).

Spawning duration of individual females

Duration of the spawning period for individual females cannot be stated with precision because cages were examined only once a week. In 1956 the average duration for 11 females was approximately 6 weeks. In 1957 for 20 of 21 identifiable females it was also 6 weeks (Table VI). The spawning period in the experimental area lasted approximately 9 weeks in 1956 and 8 weeks in 1957 (Figs. 10C and 11C). These cage data thus indicate that a single female may spawn throughout most of the spawning season.

Substratum of embryo case deposition

Types of substratum females select for depositing embryo cases were determined from 3 large hand-picked collections of shells and other objects with attached cases from the experimental area and from cages and aquaria. The most common shells in this area were dead hard clams or live clams partly exposed, and dead and live oysters. These shells supported jingles *Anomia simplex,* worm tubes *Hydroides* sp., and often growths of red sponge *Microciona* sp. Cases were always attached to hard surfaces and no preference for jingles, worm tubes, or the clam or oyster shell itself was obvious. Cases were also found on dead jingles, short razor clams *Tagelus plebius,* stones and bottles. Uncommonly, cases were found on live *E. caudata, U. cinerea, Anadara ovalis,* and *Modiolus demissus,* dead *Anadara transversa,* live and dead *Balanus* sp., and bases of eelgrass blades. In the laboratory they were found on wood, plastic screen and sheeting and metal tacks. The only evident requirements for these substrata are that

FIG. 12. Variation in shapes of *E. caudata* embryo cases collected in the vicinity of Gloucester point. X5.3.

A to H —Usually shaped cases
D —Most common shape
I to P —Unusual shapes
K —Stalk with odd wing-like protuberances
N to P —Cases with no secondary projection

they be hard and free of fouling. Occasionally *U. cinerea* cases occurred in similar sites. Most cases were deposited upright in a vertical or slightly tilted position, but a few were found distal end down. Because *E. caudata* does not climb appreciably, no cases were found on eelgrass blades or pier pilings, where *U. cinerea* cases occur in numbers.

Since new clusters were deposited in various places about cage compartments which held one female, it is apparent that females do not necessarily return to their old spawning sites to deposit cases.

Description of cases and embryos

Embryo cases of *E. caudata* are leathery, vase-shaped capsules with 2 distal projections which make them easy to distinguish from cases of other local gastropods. The larger projection is a hemispherical operculum which covers the aperture through which hatching conchs will emerge, the smaller is a solid extension of case material. The case itself is triangular in cross section. A longitudinal seam or suture extends from one side of the stalk distally along one triangular edge of the case over the operculum, dividing it into halves, and down the middle of the broad side to the opposite side of the stalk. Similar sutures in embryo cases of muricids *Thais lapillus* and *Ocenebra erinacea* were described by Fretter (1941), and in *U. cinerea* by Hancock (1956). Figure 12 illustrates variability in shapes of cases. The secondary projection is not always present and the seam does not always occur in the same plane of each case, although it always runs over the middle of the operculum. A few anomalous cases were observed with sections of walls missing, but with embryos still in normal position.

The color of cases changes with time. When first deposited they are almost translucent except for the opaque cap. They do not have the bluish cast described by Pope (1910-11), Carriker (1955), and Ganaros (1957) for cases of *U. cinerea.* In 2 or 3 weeks the color changes to deep yellow, and after the conchs have emerged, to dark brown. Cases from the experimental area averaged, in mm, 7.7 in height (6.0 minus stalk), and 1.8 in width. Range in height was 5.2 to 11.0. Cases collected at Tillage's oyster ground averaged 9.2 (6.9 minus stalk), and 2.4 wide, and ranged from 7.4 to 11.3 in height.

Whenever a female was observed depositing cases, measurements were made of her height and height of the cases. As Hancock (1959) found with *U. cinerea,* usually larger females deposit larger cases but in *E. caudata* there is considerable variation (Table IX). Perhaps measurement of the soft parts of the drill such as dimensions of the foot would have shown a closer correlation between her size and size of embryo cases she deposits.

TABLE IX. Relationship between shell height of *E. caudata* females and mean height of embryo cases they deposited, summers of 1956 and 1957 (Caged and natural populations)

Height of female (mm)	Height of cases (mm)	Numbers of cases
20.1	6.5	59
20.5	6.4	41
21.1	7.1	48
21.1	7.8	6
22.2	7.5	14
23.4	8.0	25
23.5	7.7	2
24.0	7.1	6
24.1	8.2	3
24.3	9.0	14
24.8	7.2	26
25.4	8.2	25
26.0	9.9	10
26.5	9.1	8
26.8	7.9	18
26.9	8.1	14
27.5	8.2	19
28.0	7.5	6

Measurements were made of most cases deposited by known caged females in 1956. Mean height for the first half of individual spawning seasons was 7.3 mm. Mean height in the 2nd half was 7.0 mm. The difference was not significant statistically ($\chi^2 = 32.45$, d.f. $= 22$, $P = 0.08$); therefore, there is no evidence that size of embryo cases changes during the spawning season.

Within freshly-laid cases, embryos form a loose clump suspended in a clear jelly-like substance. Early embryos are spherical and most are pale yellow, though many are white. A few are yellow, light tan, light orange or purple. Carriker (1955) stated that *U. cinerea* embryos are yellow to orange in color. Necrotic embryos usually turn purple. Live, apparently normal, protoconchs with purple vitelline bodies were seen occasionally. When locomotory organs develop, embryos move about within the case until they hatch, but late protoconchs often become so crowded that movement is impeded.

Forty-two freshly-laid embryos averaged 0.36 mm (range 0.34-0.39) in diameter, the same size reported by Carriker (1955) for *U. cinerea* embryos. Fifty-four hatching conchs, measured as they emerged from the apertures of cases, averaged 0.9 mm (range 0.7-1.1) in greatest height. The conchs are not pelagic and after emergence they crawl down the sides of their cases and about the substrate to which the case is attached. Tubular noncoiled individuals, looking otherwise nor-

TABLE X. Numbers of embryos per case in various samples collected at Gloucester Point and Tillage's oyster ground (summer 1956 and 1957)

Location	Source	Date	No. of cases	Embryos Per Case		
				Mean	Range	Variance
Experimental area	handpicked shells	May 28-30, 1957	277	12.6	1-24	17.0
" "	" "	Jun 15-17, 1957	349	13.5	2-27	16.2
" "	" "	Jul 1-22, 1957	166	13.3	1-27	18.4
" "	buoyed traps	May 28-Jun 28, 1956	210	15.8	5-35	27.7
" "	" "	Jun 1-Jul 19, 1957	187	14.5	6-32	27.4
Cage, experimental area	cage	May 24-Jun 30, 1956	262	15.2	2-32	23.6
Cage, large mixed local and Wormley Rock drills	"	Jun 9-Jul 4, 1956	184	21.2	10-37	23.3
Tillage's oyster ground	dredged oysters	May 13-Jul 2, 1956	157	18.4	6-36	30.9
" " "	" "	Jun 13, 1957	283	20.2	3-34	20.1
" " "	cage	Jul 3-24, 1956	90	19.5	8-47	49.4

mal, appeared occasionally. Although somewhat similar, late stage protoconchs of *E. caudata* from this area differ from those of *U. cinerea* in that the siphonal canal is less heavily-tinged with purple; the 2 protoconchs can usually be distinguished by this character.

Number of embryos per case

In 1935 Haskin showed that *E. caudata* in Cedar Creek, Barnegat Bay, New Jersey, deposited more embryos per case than *U. cinerea*. In traps and cages, 445 cases average 22.2 embryos each (range 8 to 42), and 1,297 *U. cinerea* cases averaged 8.1 embryos each (range 0 to 20). According to Carriker (1955), 6 similar studies of *U. cinerea* report averages varying from 8.0 to 11.0 embryos per case.

In this study, 10 samples of cases (Table X) were collected during 1956 and 1957 to determine whether (1) the numbers of embryos per case change during one spawning season, (2) there are annual variations in a particular area, (3) there are local differences between drill populations in a particular area, and (4) there are differences between caged and wild drills. The results were not conclusive except to show a clear difference between the experimental area and Tillage's ground, which suggests that there are local differences in numbers of embryos per case. Hancock (1959), working on *U. cinerea* in English waters, found quite marked differences in numbers of embryos per case from one location to another.

A small number of selected large females held in a cage deposited an average of 21.2 embryos per case, about 7 above normal for the experimental area, which suggests that characteristics of the female, rather than environmental factors, may be the more important factor controlling numbers of embryos per case.

Similar to the findings of Hancock (1959) who found that there is considerable variation in numbers of *U. cinerea* embryos per case deposited by a single female, records of individually caged *E. caudata* females also demonstrate considerable variation in this attribute (Tables XI and XII).

TABLE XI. Variation in numbers of embryos per case deposited by individual caged females, summer 1956

Female	Number of cases	Mean	Variance
A	58	11.9	5.5
B	43	9.9	6.8
C	79	8.2	3.1
D	29	20.8	11.7
E	59	10.0	4.8
F	19	18.1	16.3
G	23	14.4	6.8
H	28	16.5	20.4
I	26	10.3	3.7

TABLE XII. Variation in numbers of embryos per case deposited by female B in table 11

Number of embryos	Frequency
4	1
5	2
6	1
7	3
8	4
9	11
10	4
11	6
12	3
13	6
14	0
15	1
16	1

Incubation period

Knowledge of the incubation period of *E. caudata* embryos may be useful in developing control measures involving destruction of embryo cases. Several workers have collected data on this subject for *U. cinerea* in other areas, and their results vary widely. The most careful work has been

done by Haskin (1935), Cole (1942), and Ganaros (1958).

Haskin (1935), working in Barnegat Bay, held embryo cases in field cages at temperatures ranging from 23.3°C to 29.1°C, and reported incubation periods lasting from 18 to 25 days. Cole (1942), in England, found incubation periods of 27 to 32 days when cases were held in the laboratory at temperatures averaging 22.6°C. At Milford, Connecticut, Ganaros (1958) determined incubation periods of embryos held in the laboratory at constant temperatures. The first conchs held at 20°C were released in 30 to 43 days; those held at 25°C, in 22 to 38 days.

Embryo cases of *E. caudata* were collected from traps and a cage every 2 days, left on their original substratum, and placed in clear perforated plastic cups suspended from the laboratory pier in a tray one foot from the bottom. Two or 3 clusters containing several cases each were used for most determinations. Cases were examined every 2 days for hatching embryos. Termination of the incubation period was defined as the time when over one-half the cases in a particular cluster had released at least one conch. Although a slightly uneven rate of development was observed, no attempt was made to record incubation periods of individual embryos.

To determine whether holding cases in perforated plastic cups influenced incubation periods, oysters bearing cases were attached to a rectangular wooden board by elastic bands. Because the board collected algae, tunicates, and silt, it closely resembled the bottom.

Table XIII shows that there was close agreement in hatching times of embryos in different clusters of the same age, and that holding cases in perforated cups apparently did not influence the

TABLE XIII. Incubation periods of *E. caudata* embryos

Site	Date laid	Number of cases	Hatching date	Incubation period (days)	Temperature During Period (°C)	
					mean	range
Cup	May 18-23	—	June 15-17	24-31	21.1	18.3-24.7
"	May 28-30	—	June 19-21	21-25	23.4	19.2-24.7
	May 28-30	—	June 19-21	21-25		
	May 28-30	—	June 19-21	21-25		
"	June 11-13	12	June 29-July 1	17-21	24.7	21.9-26.9
	June 11-13	10	June 29-July 1	17-21		
	June 11-13	21	June 29-July 1	17-21		
1 "	June 18-21	13	July 5-7	15-20	25.4	21.9-27.5
9	June 18-21	8	July 5-7	15-20		
	June 18-21	3	July 5-7	15-20		
5 "	June 27-29	4	July 13-15	15-19	26.0	25.0-27.5
6	June 27-29	7	July 13-15	15-19		
"	July 5-7	4	July 20-24	14-20	25.6	25.3-25.8
	July 5-7	6	July 20-24	14-20		
"	July 14-16	11	July 29-31	14-18	25.7	25.0-26.1
	July 14-16	5	July 29-Aug. 1	14-19		
	July 14-16	—	July 29-Aug. 1	14-19		
"	July 24-26	5 or 6	Aug. 10-12	16-20	25.4	24.4-26.4
	July 24-26	5 or 6	Aug. 10-12	16-20		
Cup	May 14-16	14	June 6-8	21-25	21.7	19.4-23.1
Board	May 14-16	10	June 6-8	21-25		
Cup	June 15-17	5	June 28-July 1	12-17	26.2	24.7-27.2
1 Board	June 15-17	6	June 28-July 1	12-17		
9 Cup	June 24-26	9	July 8-10	13-17	26.1	25.3-26.7
Board	June 24-26	6	July 8-10	13-17		
5 Board	June 24-26	16	July 8-10	13-17		
7 Cup	July 4-6	13	July 19-21	13-17	26.4	25.8-26.9
Board	July 4-6	12	July 19-21	13-17		
Board	July 14-16	6	July 30	14-16	26.6	25.8-27.5

incubation period. Incubation periods lasted 24 to 31 days at a mean temperature of 21.1°C and shortened as the temperature increased, *e.g.* at 26.5°C it lasted only 15 to 17 days. Probably as a result of higher temperatures in 1957, incubation periods were shorter than in 1956. Incubation periods for *E. caudata* were 5 to 6 days shorter than those reported for *U. cinerea.*

Percentage of embryos reaching protoconch stage

Unlike *Thais lapillus* and other related gastropods (Korschelt and Heider 1890), *E. caudata* females do not include nurse embryos (nourishing eggs) within their cases. Portman (1926) and others believe that nurse embryos are produced by fertilization of normal ova by atypical spermatozoa. Evidently such embryos fail to develop normally and serve as food for normal embryos. Nurse embryos were not seen in the almost 3000 cases studied, and microscopic examination of gonad smears of hundreds of males of *E. caudata* showed only one type of spermatozoon.

To establish the numbers of embryos that successfully attain the prehatching or protoconch stage, embryos in 37 freshly-deposited cases were counted by carefully manipulating cases under the lens of a binocular microscope. Cases were then isolated in separate compartments of a plastic box held in an oyster tray suspended in the York River. An average of 93% (range 82-100) of embryos in these different cases developed fully and the numbers of embryos at various embryonic stages were similar in 361 embryo cases deposited in cages.

Predators and associates of embryo cases

Large numbers of cases from the experimental area were devoid of embryos even though the operculum was still in place. Closer observations revealed holes in the sides of these cases, the most common of which was a C-shaped slit about 0.8 millimeters in diameter and, therefore, large enough to serve as possible exit for emerging conchs. At least one case with a slit still contained undeveloped embryos which indicates that predators made the slits. No evidence beyond this, however, was obtained to show whether C-shaped slits are made by the conchs themselves or by predators. Less frequently, round or oval holes of varied sizes, always too small to permit the exit of conchs, were seen. Occasional cases bore jagged tears and in some of these most of the case was torn away. In the laboratory, mud crabs (Xanthidae) made similar jagged tears. Some clusters exhibited all three kinds of damage and often more than one slit or hole was seen in a single case. Since 19 to 42% of cases in samples were damaged, predation, if this accounts for all damage, may be an important factor in limiting the size of drill populations in the experimental area (Table XIV). It is possible that predators of cases may be non-selective and prey on embryos at all stages of development. If so, many embryos still not hatched in the cases collected might have been destroyed in like manner had they been left on the bottom.

Hancock (1956) in England showed that if embryos of *U. cinerea* as old as unshelled veligers are removed from their cases, the operculum of these cases will eventually come free. The operculum will not come free if younger embryos are removed. If this is also true for *E. caudata,* it probably explains the finding of some damaged cases with their opercula missing. It seemed possible that predators might have entered empty as well as full cases; instead, they probably fed on unshelled veligers or protoconchs.

A substantial but incomplete list was made of plants and animals observed on *E. caudata* embryo cases during the summers of 1956 and 1957 (Table XV). The scale worm *Lepidonotus sublevis,* an active predaceous annelid, is one of the possible predators, though it did not appear to be common. Its scarcity, however, may be due to its ability to escape collection with cases or it may not be abundant in this area. Perhaps only a few are required to do significant damage. An as yet unidentified polychaete worm which builds a tube on embryo

TABLE XIV. Numbers of damaged and undamaged embryo cases collected by handpicking shells in the experimental area, summer 1957

Sample	Number Damaged					Number Undamaged						
	C-shaped slit	Hole	Tear	Not determined	Total	Pre-veliger stage	Unshelled veliger stage	Pro-toconch stage	Embryos hatched	Total	Total Cases	% damaged
June 15	52	21	17	15	105	135	107	113	85	440	545	19.3
June 17	179	44	0	8	231	49	127	115	43	334	565	40.1
June 26	37	6	14	0	57	52	0	16	12	80	137	41.6
July 1-22	12	9	28	0	49	15	13	2	69	99	148	33.1

cases also is suspected. *Caprella* was seen commonly about cases but did not damage them in the laboratory. Possibly the gastropods *Bittium alternatum,* small *U. cinerea, Mitrella lunata, Odostomia impressa,* or other gastropods, worms or small arthropods common on oysters and eelgrass, but rarely seen on cases, perforate them. Occurring commonly on cases with slits or holes, often several on one drill case, were embryo cases of 2 small gastropod species. In the laboratory these cases released pelagic veligers which did not survive to a stage that could be identified.

TABLE XV. Plants and animals observed attached or clinging to *E. caudata* embryo cases

	Occurrence
Ulva sp.	Common
Small filamentous multicellular brown algae	Common
Various diatoms	Abundant
Folliculina moebiusi	Rare
Zoothamnium sp.	Abundant
Yellow sponge	Common
Red sponge on base	Rare
Sea anemones	Rare
Nematodes	Abundant
Feather-duster worms (two species)	Rare
Lepidonotus sublevis	Rare
Unidentified burrowing polychaeta	Common
Young *Balanus* sp.	Once
Caprella sp.	Common
Bittium alternatum	Rare
Urosalpinx cinerea early conch	Rare
Mitrella lunata near base of cases	Rare
Odostomia impressa	Rare
Three types of gastropod embryo masses	Two very common; one rare
Colonial bryozoa	Common
Molgula sp.	Rare

Folliculina moebiusi, the bottle animal, occurred on several cases in one cluster. *Zoothamnium,* a colonial protozoan, occurred in large numbers on many. A yellow sponge was seen commonly around the bases but few clusters were completely covered by it. Small anemones were seen 3 or 4 times. Nematodes and diatoms were abundant in the detritus which collects on cases. Two species of feather-duster worms which make coiled tubes occurred only rarely. A young barnacle was also observed. Cases were commonly partially encrusted with colonial bryozoa, and young *Molgula* were occasionally attached. Probably none of the above listed organisms except the yellow sponge seriously impedes development of *E. caudata* embryos.

SUMMARY AND CONCLUSIONS

Eupleura caudata, a boring snail that occurs in considerable numbers in some parts of Virginia and elsewhere along the Atlantic coast, has been investigated only spasmodically, usually in conjunction with investigations of the more widespread *Urosalpinx cinerea.* Recent studies at the Virginia Fisheries Laboratory have made it possible to outline the life history in some detail.

Because in winter few drills can be collected on traps and caged animals are dormant, it is believed that *E. caudata* hibernates. Drills in the York River become active and begin copulating in April as temperatures rise to over 10°C. Individual copulatory acts may last about 4 hours but couples often remain paired and copulate intermittently for 24 to 48 hours. There is good evidence to show that sexual promiscuity occurs. Sex ratios obtained from trap catches indicate that equal numbers of males and females move to shells projecting above the bottom during this period. Spawning begins in late May when temperatures reach 18 to 20°C, reaches a peak in June and early July (21.1° to 26.1°C), and ceases for the year about the beginning of August. During the spawning period, females come to traps in greater numbers than males. Copulation ends early in July, but is resumed in fall as water temperatures decline to about 21°C, and ceases for the year at about 16.7°C. Since females isolated after this period are capable of depositing cases with living embryos, it seems probable that this fall copulatory period serves to insure that females, particularly in sparse populations, have spermatozoa for spawning the following year.

Mature females in cages deposit an average of 55 embryo cases over an average period of 6 weeks, almost the full extent of the spawning period. Cases in the experimental area are deposited primarily on dead and live hard clams, oysters, and jingles. Most clusters include 8 to 10 cases, containing an average of 14 embryos. Ninety-three % or more of these embryos reach the protoconch stage and probably all protoconchs hatch. In the absence of predation, therefore, a mature female may produce 700 young conchs each summer. At the time of peak spawning in mid-June, the incubation period is from 12 to 20 days. Thus, the greatest emergence of conchs occurs during the first week of July when oysters begin setting at Gloucester Point (Andrews 1955).

Growth of newly hatched drills, which emerge at a height of about 0.9 mm, is apparently rapid, for their mean height on October 27, 1956 was 12 mm. Females probably are not mature in their 2nd summer, but continue to grow until the 3rd when probably most attain sexual maturity and growth ceases. The onset of maturity may be governed by rate of growth rather than by age. Males also show determinate growth, but cease growth at a smaller size. With increase in age,

sculpturing of shells is worn, and drills in their 2nd summer apparently can be distinguished from those in their 3rd or later years of life. By fall the new or zero year class also can be distinguished from the other 2 groups on the basis of shell characters.

Trap catches of drills rise to a peak about 3 weeks before the peak of spawning. Federighi (1931), Galtsoff *et al.* (1937), Stauber (1943) and Andrews (1956) noted a similar pattern in their studies of *U. cinerea.* As spring temperatures rise, the first activity of *E. caudata* is copulation, soon interspersed with feeding, which later becomes the dominant activity. This heavy feeding possibly provides energy and food reserves for spawning.

This study has revealed that females of *E. caudata* do not attain sexual maturity until after the 2nd summer of life. The species apparently compensates for this during and after its 3rd summer by depositing large numbers of cases containing many embryos most of which hatch. The species thus could be partially controlled by intensive eradication practices during the first 2 years of life. If predators of cases can be identified, and their numbers increased on natural bottom, or related forms with similar feeding habits introduced, control may be possible.

Another factor which may hold populations of *E. caudata* in check is the inability of drills to use eelgrass, pier pilings and other elevated structures as sources of food and embryo case attachment. Perhaps this explains the scarcity of *E. caudata* in the experimental area, an eelgrass bed with few shells, in contrast to an abundance of them on an abandoned oyster bar, Wormley's Rock, observed by Andrews (1956).

There is good evidence that the intensity of spawning varies greatly. Possibly, intensity of spawning is directly dependent upon intensity of copulation since both were high in 1956 and low in 1957 or, perhaps, spawning is affected by other factors which affect copulation in a similar way. Perhaps spawning intensity could be predicted in advance from a record of copulatory activity in spring.

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GREAT LAKES RESEARCH DIVISION

APPLICATIONS OF DATA COLLECTED ALONG SHORE TO CONDITIONS IN LAKE ERIE

1960

GREAT LAKES RESEARCH DIVISION

The Great Lakes Research Division (formerly Great Lakes Research Institute) is part of the Institute of Science and Technology of The University of Michigan. The Great Lakes Research Institute was established by action of the Board of Regents on May 16, 1945, for the "encouragement and integration of studies of the physical, chemical, biological, and other aspects of the Great Lakes and related areas," and was reorganized as a Division of the Institute of Science and Technology on April 1, 1960.

It is a research organization in the broadest sense, whose objectives are the stimulation, promotion and coordination of research on the Great Lakes, as well as the implementation of the University's teaching and research program for graduate students. The Division's objectives may be more specifically stated as follows:

1. To contribute by every means at its disposal to increase understanding of all aspects of the Great Lakes region.
2. To cooperate with other organizations on the campus, within the state, and outside the state in the conduct of mutually beneficial research on the Great Lakes and their tributary waters.
3. To make available the results of Great Lakes investigations, and to make special efforts to place them in the hands of those concerned with practical operations.
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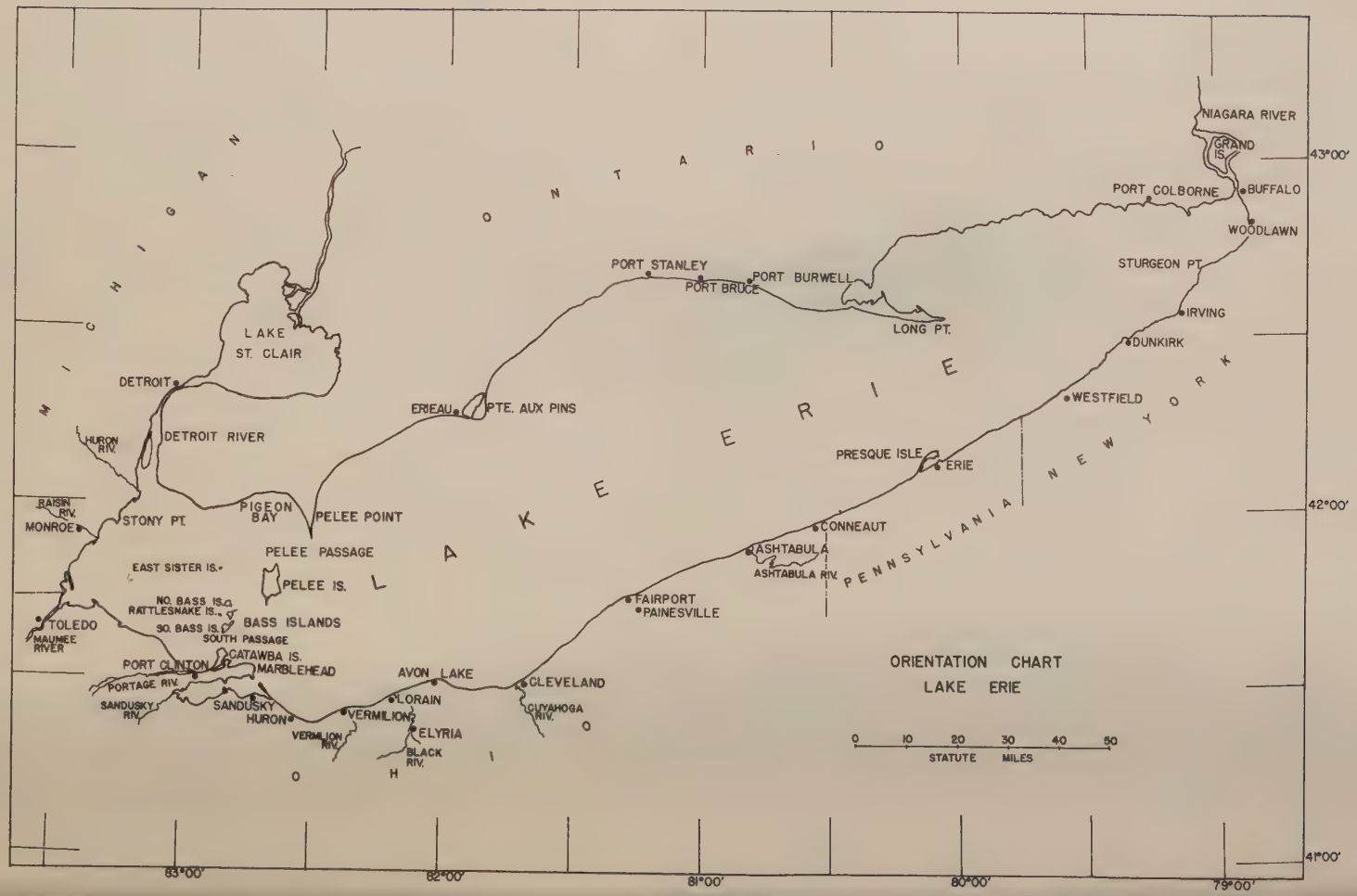
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SO. BASS IS.
BASS ISLANDS
SOUTH PASSAGE
TOLEDO
MAUMEE RIVER
PORT CLINTON
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MARBLEHEAD
PORTAGE RIV.
SANDUSKY RIV.
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PAINESVILLE
ASHTABULA
ASHTABULA RIV.
CONNEAUT
PRESQUE ISLE
ERIE
WESTFIELD
DUNKIRK
IRVING
STURGEON PT.
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APPLICATIONS OF DATA COLLECTED ALONG SHORE TO CONDITIONS IN LAKE ERIE

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INTRODUCTION

In 1957 the Great Lakes Research Institute,* under a contract with the U. S. Department of the Interior, Fish and Wildlife Service, undertook to locate sources and reprositories of limnological and meteorological data pertaining to the Great Lakes which might be useful in developing a better understanding of the physical, chemical, and biological properties of these extremely important bodies of freshwater. It was believed that a great deal of incidental limnological data might be available from agencies, in both the United States and Canada, which routinely make use of lake water. Such agencies were expected to include municipal water treatment plants, disposal plants, power plants, and industries, as well as various governmental organizations. Meteorological data were also known to be collected, in varying degrees of intensity, by many of the above-mentioned installations as well as by regular weather observers. In view of these considerations, it was desirable that the location and evaluation of such data become the object of a special initial study.

The first study (Phase I) was a search designed to locate and determine the extent of limnological and meteorological records in the Great Lakes area. The results have been reported (Powers *et al.*, 1959). A total of 1129 sources of potentially usable limnological and/or meteorological data were located within the drainage area of the Great Lakes. Prior to this study, little was known specifically about the availability, extent, and reliability of data obtained by lake water users.

The large number of data sources indicated the desirability of additional study to determine the usefulness of such data in Great Lakes studies. To this end a pilot study (Phase II) was carried out in which data from onshore and near shore sources were examined for compatibility with offshore cruise data. Determination was made of which data sources were most nearly representative of open-lake conditions, and assessment was made of methodologies, instrumentations, and other aspects influencing the accuracy and/or representativeness of the data as applied to conditions in the open lake. The pilot study was carried out on Lake Erie, and consisted of actual application of data from onshore sources to the problem of obtaining a better understanding of the hydrography and aquatic environment.

From the pilot study determinations of representative data sources were developed for each of the three basins of the lake. From it has come a new and better concept of the current pattern of Lake Erie. In addition, series of data and techniques were found by which it is possible to reconstruct several aspects of the environment from the present well back into the nineteenth century.

A major portion of this study was given to the determination of "representative stations." These are water plants or other water-user installations where data are taken routinely and whose data are representative, in known degrees, of open-lake water. The concept of the representative station as a source of data wherein trends in the condition of the aquatic environment can be conveniently and economically watched is not a new one, but it is believed that here for the first time are presented a series of realistically-appraised, representative

*Now the Great Lakes Research Division of the University of Michigan's Institute of Science and Technology.

stations for a Great Lake. Once calibrated to open-lake conditions as is done here, these stations provide the means for continuous and continuing studies of environmental factors that bear upon fishery problems as well as upon the limnology and hydrography of the lake.

The authors extend their sincere thanks to the following persons who contributed greatly to the success of this study:

Prof. D. M. Scott of the Department of Zoology, University of Western Ontario, London, Ontario, gave permission to publish the station data of the Fisheries Research Laboratory of the University of Western Ontario. Located at Erieau on Point aux Pins, and receiving financial support from the Research Council of Ontario, this laboratory carried out valuable limnological investigations in west- and north-central Lake Erie in the years 1947-53. These data are given in Appendix II. They have been extremely valuable in our studies and we believe that others will welcome their publication as genuinely as we welcomed the chance to borrow them.

Mr. Homer Knox, Ohio Department of Health; Mr. T. L. Vander Velde, Michigan Department of Health; and Mr. W. C. Kurtz, Erie County (New York) Water Authority, generously made available the water quality records of the various filtration plants. These records contained the onshore data utilized in the determination of representative stations.

Mr. Russell Johnson, Michigan Department of Health, authorized the use of studies made by him which indicate the presence of a representative shore station on Lake Michigan.

The authors also gratefully acknowledge the use of facilities of the University of Michigan Biological Station during a portion of this work.

The studies included in both Phase I and Phase II were supported in their entirety by U.S. Fish and Wildlife Service Contract No. 14-19-008-9381.

SELECTION OF REPRESENTATIVE STATIONS

Lake Erie is divided into three basins: the west basin, extending to the Bass Islands; the central basin, lying between the Bass Islands on the west and Long Point on the east; and the east basin, between Long Point and Buffalo. A logical beginning to the selection of representative stations seemed to be on the basis of these geographical areas, that is, representative stations might be found for each of the basins.

AVAILABILITY AND ACCURACY OF DATA

Two separate categories of water quality data were needed: data obtained on untreated lake water by the water-user plants, and observations obtained by some other agency from the open lake at the same time. The bulk of the information obtained by the plants consists of turbidity, total alkalinity, and bacterial counts, with water temperatures being observed at a few plants. No satisfactory method of utilizing bacteriological data being found, efforts were made to obtain open lake turbidity, alkalinity, and water temperature data. A limited body of data representative of open lake conditions, and usable in the selection of representative stations, was assembled. These data are summarized in Table I.

As previously noted, Powers *et al.* (1959) have tabulated the filtration plants and other sources of data on raw lake water, along with their periods of record and the types of data taken. Methodology varies among the plants. Total alkalinity is always by titration, usually with methyl orange as the indicator. Turbidity is generally obtained with the Hellige Turbidimeter, but the Jackson Candle and bottle standards are also in use. Visits were made by the investigators to most of the Lake Erie plants. In all cases the operators, superintendents, and chemists were impressive in their general attitudes, methods, and awareness of responsibility. It is believed that consistency of results may safely be assumed within individual plants.

Permanent records from the filtration plants are maintained in reduced form, indicating for each month the average (and usually the maximum and minimum) value for any measured parameter. In Michigan and Ohio, these records are on file with the state departments of health. Woodlawn, New York, records are retained at the plant. Data for Erie, Pa., are published annually.

Scarcity of lake water data from Canadian filtration plants utilizing Lake Erie water restricted the search for representative stations almost entirely to the south shore of the lake.

The selection of representative stations was a two-fold operation depending, first, upon a determination of the average surface current pattern (which would indicate those stations where offshore water came to shore) and, second, upon simultaneous shore station and open lake physical-chemical data that could be compared to give definitive assessments of the representativeness of stations apparently sampling water from offshore. Initial efforts were directed at the determination of the average surface current pattern existing under the prevailing southwesterly wind. This pattern would be the one expected to occur the majority of the time.

SURFACE CIRCULATION OF LAKE ERIE

Although complete synoptic coverage of Lake Erie has never been reported, sufficient data have been collected from a number of sources to attempt a synthesis

Table I. Summary of Open-Lake Physical-Chemical Data Usable in the Evaluation of Representative Onshore Stations

Source	Years and Region	Applicable Data
Parmenter (1929) Fish (1960)	1928: east basin 1929: east and central basins	Methyl orange, phenolphthalein alkalinity; turbidity; water temperature; wind speed and direction
Chandler (1940, 1942a, 1942b, 1944, plus unpublished data); Chandler and Weeks (1945)	1938-45: Bass Islands (West basin)	Methyl orange, phenolphthalein alkalinity; turbidity; water temperature
D. M. Scott, University of Western Ontario, London[1]	1947-53: central basin	Methyl orange, phenolphthalein alkalinity; water temperature
U. S. Fish and Wildlife Service (1958a, b; 1959)	1958: west basin, plus drift bottle returns from central and east basins	Total alkalinity, turbidity, silica, magnesium, sodium, water temperature, wind speed and direction

[1]Data published here (Appendix II).

of a composite pattern of surface circulation. The pattern as derived appears to be one which could be generally representative of the surface currents existing under the normal regimen of prevailing southwest winds.

The data sources utilized in the present synthesis, together with the specific portions of the lake which they represent, are as follows:

1. West end: Ayers (unpublished), Harrington (1894), Millar (1952), Olson (1951), Verber (1955), Wright, Tiffany, and Tidd (1955), U. S. Fish and Wildlife Service (1958a, b; 1959).
2. Bass Islands to Dunkirk: Fish (1960), Harrington (1894), U. S. Fish and Wildlife Service (1958a, b; 1959).
3. Dunkirk to Buffalo: Fall (1910), Harrington (1894), McLaughlin (1911), Parmenter (1929), U. S. Fish and Wildlife Service (1958a, b; 1959).

The data of Fish (1960) were collected in 1928 and 1929 during several cruises of the vessel "Shearwater" in the east and central basins of Lake Erie. The data of Parmenter (1929) were obtained during the 1928 cruises, and apply to the east basin only. Of Fish's 1929 data, those collected during Cruise 2 (made in June) have been particularly applicable to the synthesis of a current pattern under normally prevailing winds. Between the Bass Islands and Dunkirk most of the stations were occupied under winds from westerly quarters; exceptions were stations 43-46 (wind "south zero to calm") and stations 32-37 ("wind southeast 2 to calm"). Between Dunkirk and Buffalo winds were from easterly quarters, and data from that area have not been utilized here.

Data from the several remaining cruises made by the "Shearwater" in the summer of 1929 were not suitable for incorporation into an analysis of the circulation because variable winds were encountered during each cruise.

Observations of temperature from "Shearwater" Cruise 2 have been used in the computation of dynamic heights, by the method of Ayers (1956) and Ayers and Bachmann (1957), over that portion of the lake between Cleveland and Dunkirk. Although temperatures at each station were obtained at only surface, ten meters, and bottom, the lack of thermal stratification in early June allows fairly accurate interpretations of vertical temperature structure based upon these relatively few data. A reference level at only twenty decibars was required by the shallowness of the lake, and the assumption of no motion at this depth is probably not altogether realistic. However, the computed dynamic topography (Fig. 2) appears reasonable and is consistent with other parameters. Plots of turbidity and total alkalinity, as observed during Cruise 2, have been used as supplementary evidences of circulation patterns. Preliminary analyses of drift bottle returns from releases made by the U. S. Fish and Wildlife Service during 1958 and by Harrington in 1892 and 1893 have been used extensively in checking the computed current pattern between Cleveland and Dunkirk, and in deduction of the circulation pattern in the western and eastern ends of the lake where no dynamic calculations were possible. Other sources, to which reference has already been made, were consulted in the analysis of the west basin circulation. The final current pattern as synthesized from all data is given in Figure 1.

Description of Data.—The usual description of data is not feasible, since the results of numerous workers have been used. For the most part, necessary description is incorporated into the presentation of the deduced composite circulation. The returns of the Fish and Wildlife Service (hereafter referred to as FWS) drift bottle releases of May and August 1958 merit special consideration, for certain features of their distributions have particular significance.

In May, FWS drift bottles released at stations northwest and north of Pelee Island stranded in three regions: on the west side of Pelee Point; between Port Burwell and the tip of Long Point; and on the south shore between Irving, N. Y., and Buffalo. In addition, one bottle was recovered on Grand Island in the Niagara River. Bottles released in the same longitude, but south of the north end of Pelee Island, were recovered on the south shore between Catawba Island and Dunkirk, New York, with a few stranding in the Bass Island. None of these bottles were recovered from the north shore. A further feature of the south shore recoveries was the concentration of returns between Catawba Island and Fairport, and the virtual absence of returns from Fairport to the Pennsylvania-New York state line. Only one bottle was found (at Erie, Pa.) in this otherwise barren region, although returns were obtained from the New York shore farther east. Special note should be taken of the fact that bottles released north and south of Pelee Island remained completely separated, except along the New York shoreline where bottles from both areas of release were recovered.

In August the pattern of returns was quite similar to that of May. The differential north shore-south shore pattern was still present, the primary difference being that the line of demarcation between north-shore-stranding stations and south-shore-stranding stations had shifted to the south. The line now lay slightly south of the southern end of Pelee Island. Bottles from north shore stations were again found at Pelee Point, between Port Burwell and the tip of Long Point, and on the south shore between the Pennsylvania-New York boundary and Buffalo. In addition, bottles were recovered from Point aux Pins, Grand Island, Port Colborne, and between Pelee Point and Point aux Pins. Bottles from all remaining stations in the Bass Island longitude beached on the south shore, predominantly between Fairport and Conneaut. Absence of returns from the region between Conneaut and the Pennsylvania-New York line was again evident; only a single bottle recovered

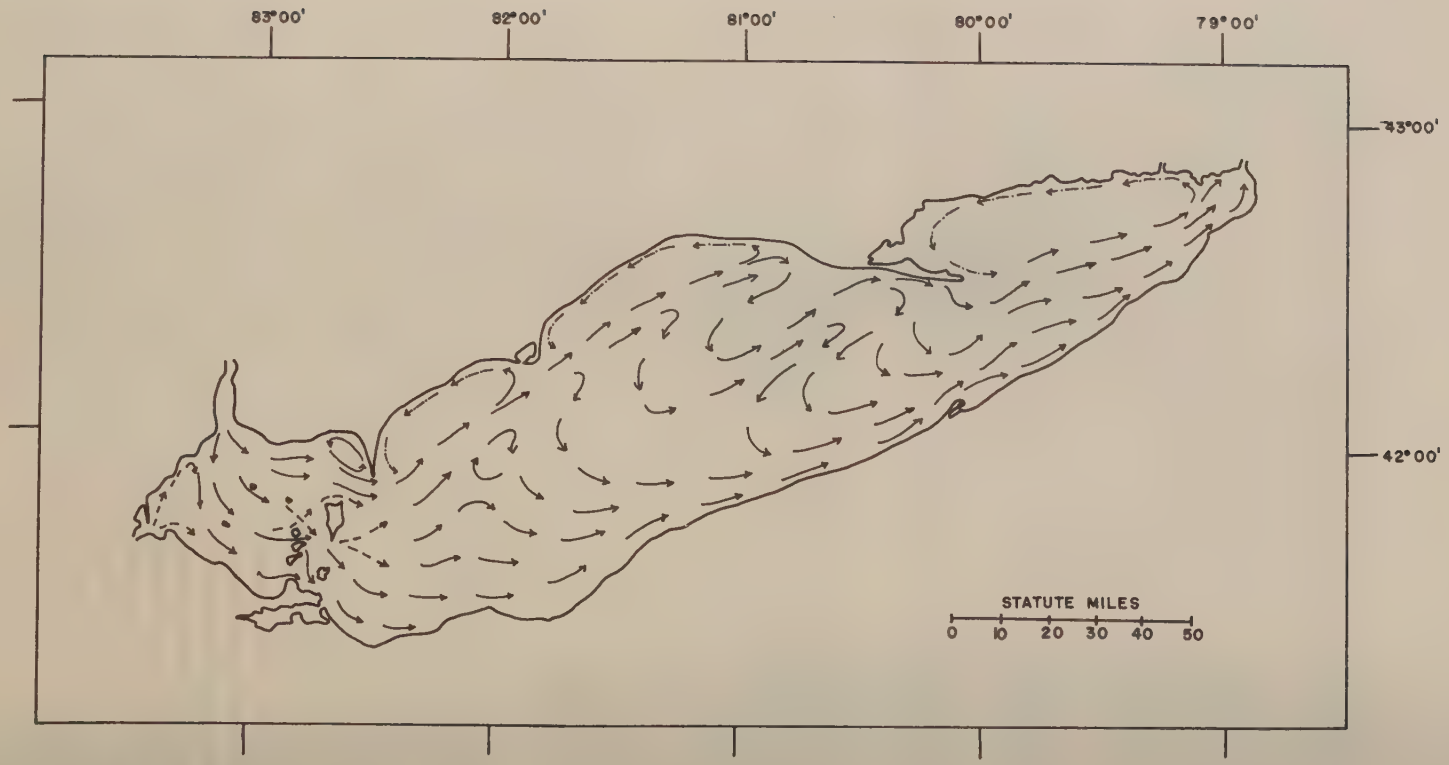

Fig. 1. Composite surface circulation, Lake Erie, under prevailing winds.

at Erie, Pa., appeared in this otherwise recoveryless stretch of shoreline. Bottles from two of the south shore stations progressed beyond Conneaut: those from one station off Marblehead beached at Erie and at Sturgeon Point, N. Y.; those from a station just west of Catawba Island beached at the Pennsylvania-New York line, near Port Colborne (Ontario) and on Grand Island.

Recoveries from drift bottle releases made by Harrington in 1892-93 coincide well with those of the 1958 FWS releases. With the exception of one bottle that stranded on the shore of Pigeon Bay (in the west basin), none of his bottles released in the Bass Islands region south of Pelee Island beached on the north shore. Also, the same south shore hiatus as observed in the FWS returns was evident: only one return was obtained from the shore between Conneaut and Westfield.

Description of the Circulation.—Investigations in the west basin of Lake Erie have indicated the circulation there to be complex and variable. Under the normally prevailing southwesterly winds, the effluent of the Detroit River usually swings through the basin in a counterclockwise loop. This water, identifiable by its comparatively low turbidity and alkalinity (U. S. Fish and Wildlife Service 1958a, b; 1959) is commonly observed passing eastward through Pelee Passage, extending at times as far south as West Sister Island. South of Pelee Island increased turbidity, alkalinity, and hardness indicate the presence of admixed waters from the Maumee River, Huron, Raisin, and Portage rivers. This mixed water ordinarily passes east through the Bass Islands. The boundary separating the unmodified Detroit River water from the mixed water fluctuates in geographic location, being strongly and rapidly influenced by changes in direction of wind.

The outflow from Pelee Passage apparently moves to the northeast toward Point aux Pins and along the lakeward side of a tentative counterclockwise eddy lying in the embayment between Pelee Point and Point aux Pins. This eddy is supported by two FWS bottles, released in August 1958 just southwest of Pelee Point, which stranded halfway between Pelee Point and Point aux Pins, and by the very existence of the two points themselves which could be both built and maintained by such an eddy circulation. Three bottles released near mid-lake by Harrington were recovered on the beach west of Point aux Pins; they likewise point to the existence of this eddy. Current features outlined in the above two paragraphs are shown in Figure 1.

The main line of current flow continues northeast past Point aux Pins, toward Port Burwell, and passes along the outside of a counterclockwise eddy lying in the embayment between Point aux Pins and Port Burwell. This eddy, also considered tentative, is confirmed by two FWS bottles released in August 1958 just southwest of North Bass Island and which stranded near Port Bruce, and by two of Harrington's bottles: one from just south of Pelee Point which stranded west of Port Stanley, and one released south-southwest of Port Stanley near mid-lake and recovered at Point aux Pins.

Southwest of Port Burwell the main current impinges on shore in an area marked by concentrated bottle returns from FWS "north shore" stations. This impingement is indicated by the tongue-like extension of the dynamic height contour of 20.011 (Fig. 2), by the area of < 3 ppm turbidity extending northeast to this point (Fig. 3), and by the 102 ppm contour of total alkalinity (Fig. 4). It is also the site of beaching of two of Harrington's bottles which were released north of mid-lake off Point aux Pins.

After impinging on Long Point, the current is indicated by the dynamic computations as turning southwest away from shore, to mid-lake, thence northeast again to Long Point at an area several miles southeast of the initial impingement. The return of the current to this region is substantiated by another concentration of FWS bottles released near mid-lake southwest of Pelee Point; by the northeast

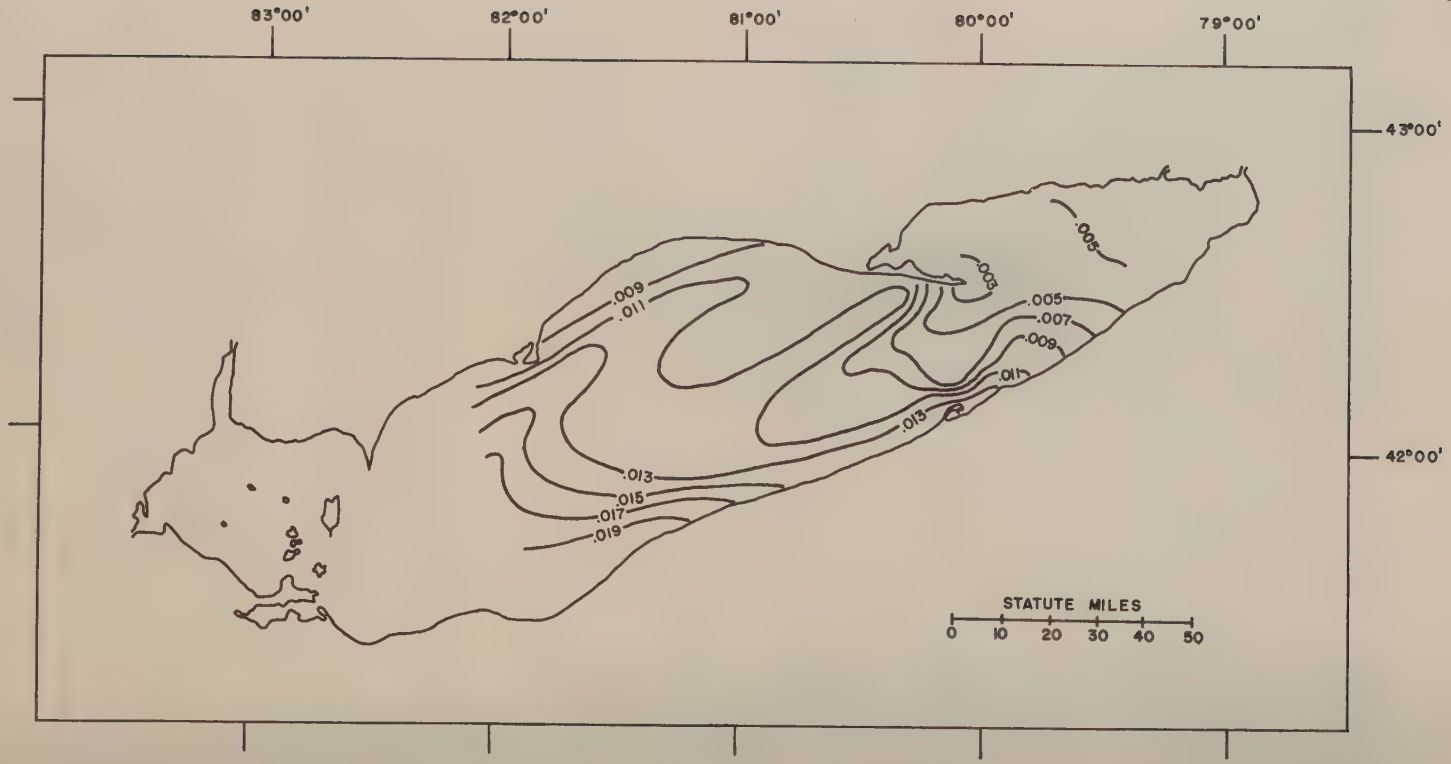

Fig. 2. Dynamic topography of lake surface referred to the 20-decibar level. (Computed from data of "Shearwater" Cruise 2, June 1929.)

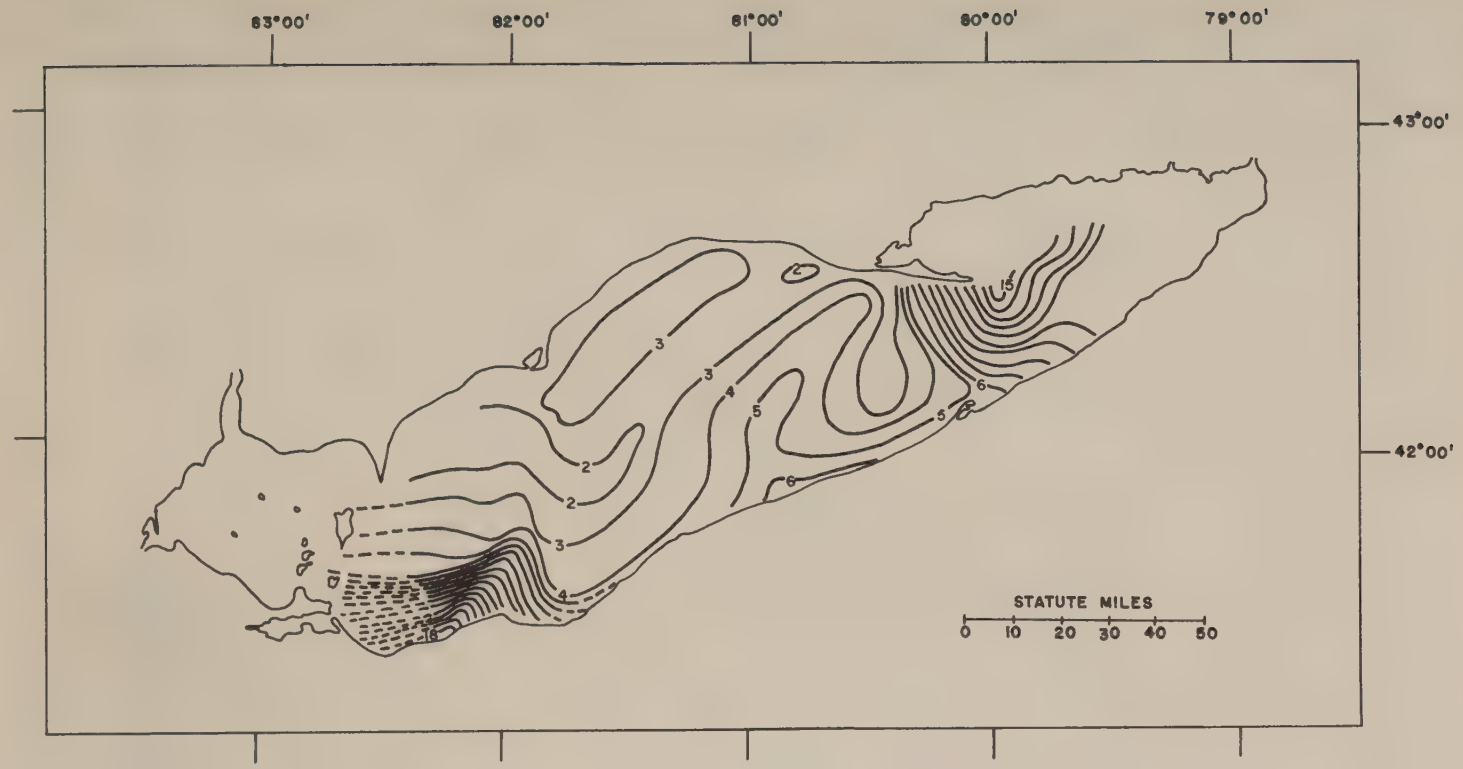

Fig. 3. Surface turbidity, ppm. (Drawn from data of "Shearwater" Cruise 2, June 1929.)

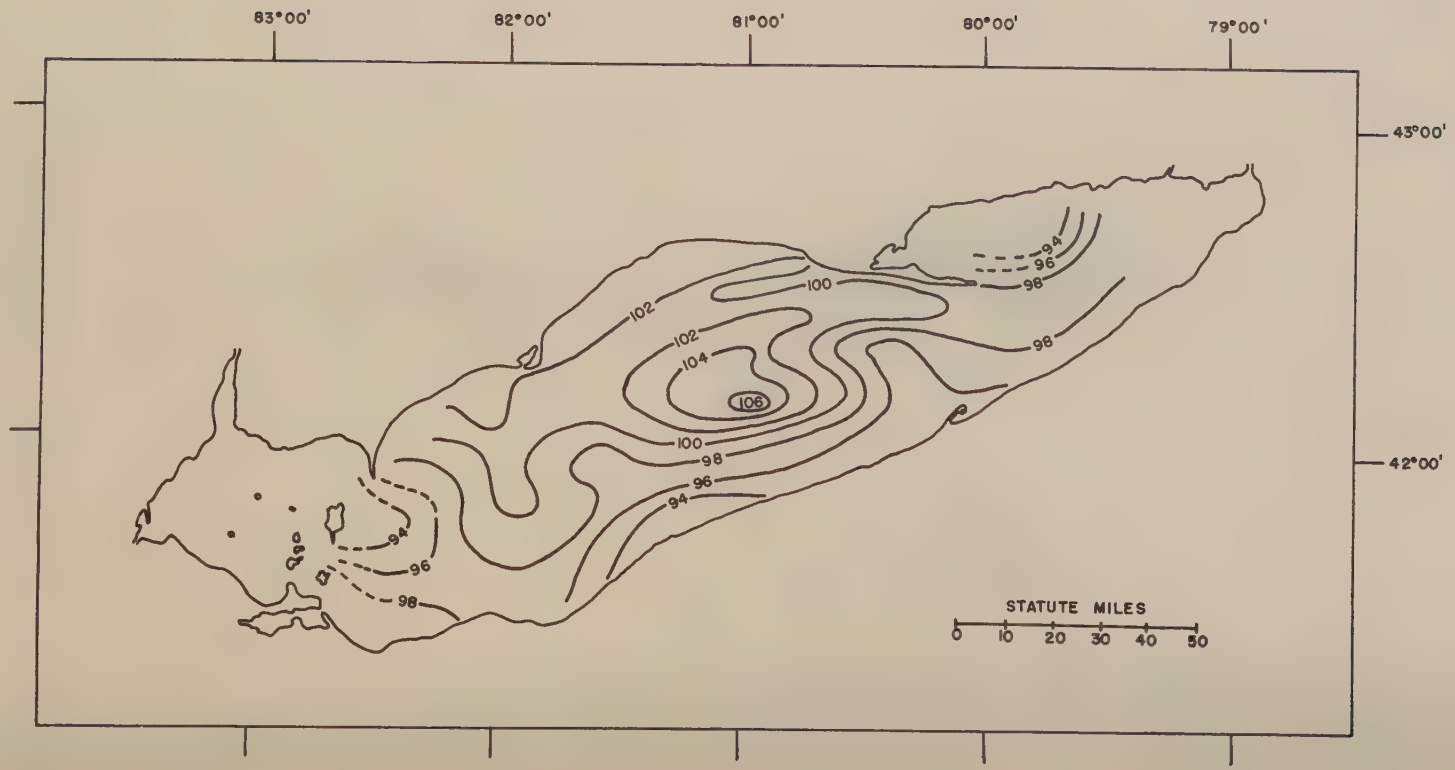

Fig. 4. Surface total alkalinity, ppm. (Drawn from data of "Shearwater" Cruise 2, June 1929.)

extension of the 3 and 4 ppm contours of turbidity extending from mid-lake (Fig. 3); and by the extension shoreward of a < 102 ppm area of total alkalinity located in mid-lake (Fig. 4).

After its second impingement on Long Point, the current appears to flow southeast along the Point before once again swinging away from shore, southwestward, to cross the lake. In the region off Ashtabula it encounters an eastward flow along the south shore. The southwestward recurving of the 3 and 4 ppm contours of turbidity (Fig. 3) support the dynamics in indicating this southwest flow.

The southern alongshore current appears to have originated partly as the outflow from the west basin through the Bass Islands, and partly as a southeast offshoot of the main current through Pelee Passage. The dynamic heights (Fig. 2) indicate a southeast current originating south of Point aux Pins, and such a flow is also suggested by the southeast curving of the contours of turbidity (Fig. 3) and total alkalinity (Fig. 4) in that region. Evidence for the alongshore current emanating from the island region is obtained from FWS drift bottle returns from releases at "south shore" stations, where beaching occurred all along shore from Catawba Island to Conneaut; from the lobate gradient of turbidity, with values increasing toward the west, situated off Lorain and Cleveland (Fig. 3), and by the 98 ppm contour of total alkalinity leading from the Bass Islands and beaching near Lorain (Fig. 4). Numerous bottles released by Harrington also were recovered along the south shore, particularly between Cleveland and Conneaut.

The eastward current along the south shore near Erie, Pa., appears to have the effect of holding offshore the current arriving from the north side of the lake. The dynamic height contours of 20.011, 20.090, and 20.070 dynamic meters extend southwest from Long Point, recurve to parallel the axis of the lake, and then come to shore east of Erie (Fig. 2). The suggestion that this current remains offshore between Conneaut and the vicinity of the Pennsylvania-New York line is substantiated by the lack of drift bottle returns from this section of shore in the results of both Harrington and FWS. It is also suggested by the shape of the 98 ppm contour of total alkalinity (Fig. 4), and by the 5 ppm contour of turbidity (Fig. 3) which remains offshore to the vicinity of Erie, where it encounters an east-west gradient with isopleths beaching east of Presque Isle.

East of Long Point and Erie the circulation pattern is somewhat conjectural. Data obtained in this region during the summer of 1928 (Parmenter, 1929) indicate an eastward surface movement extending from the central axis of the lake to the south shore, continuous to the outlet at the Niagara River. Drift bottle returns of Harrington and FWS support the existence of this movement, and Fall (1910) and McLaughlin (1911) show the eastern parts of such a flow. Parmenter's data also suggest that easterly winds can bring about a reversal of this condition, but the frequency of such a reversal and its effect on the circulation of the central basin cannot be assessed from available information.

In the embayment to the east of Long Point there is evidence of a counterclockwise eddy. This evidence is furnished by several of Harrington's drift bottles which apparently followed a counter (westward) flow along the Canadian shore between Port Colborne and Long Point. Also, two FWS bottles released in August were recovered at Port Colborne. The northward recurving of the eastward portion of the turbidity gradient located south and southeast of Long Point (Fig. 3), as well as the curvature of the 98 and 94 ppm contours of total alkalinity extending eastward from Long Point (Fig. 4) are further suggestions of eddy motion in this area.

REPRESENTATIVE STATIONS FOR THE WEST BASIN

It might initially be expected that a station representative of open lake conditions in the west basin would be one of those located on the shores of this basin, that is, the filtration plants at Monroe, Toledo, or Port Clinton. None of these plants were usable, however, because each reflects the conditions of a localized water source and not the mixed product of the several sources contributing to the west basin. As mentioned, the circulation in this basin is complex and variable. Depending upon the wind, Monroe's intake off Stony Point usually samples either Detroit River or Maumee River water (see dashed arrows, Fig. 1) but may at times be largely affected by the effluent of the River Raisin which enters the lake at Monroe south of the intake (Ayers, 1958). The Toledo intake, being located near the mouth of the Maumee River, samples proportionately large amounts of water from this source. The Port Clinton intake located just off the mouth of the Portage River largely reflects conditions of the river water rather than those of the lake. Knowledge of physical-chemical conditions existing in the Maumee and Portage Rivers was obtained from data of the Lake Erie Pollution Survey Supplement (State of Ohio, 1953).

Since the generalized circulation pattern shows the presence of an eastward flow along the south shore of the lake and indicates that this flow might consist of the mixed effluent from the west basin, it appeared reasonable to continue the search for a station representative of the west basin by using data from filtration plants located on the south shore to the *east* of the Bass Islands. Such south shore plants are at Sandusky, Huron, Vermilion, Elyria, Lorain, Avon Lake, Cleveland, Fairport, Painesville, Ashtabula, and Conneaut.

The Data.—Data obtained by D. C. Chandler in the Bass Islands region between September 1938 and December 1945 (Table I) were considered to be adequately representative of west basin water. A number of parameters were observed, but for purposes of the present investigation turbidity and total alkalinity were the most applicable; these parameters were consistently measured by the filtration plants. Periods and locations of Chandler's observations are as follows:

(1) Total alkalinity: September 1938 to October 1940, at a single station just off the west side of Rattlesnake Island; February 1943 to December 1945, at four stations located in a north-south direction: one just northeast of East Sister Island, one just west of North Bass Island, one at Rattlesnake Island (identical with the one used in the 1938-40 series), and one in South Passage between Catawba Island and South Bass Island.

(2) Turbidity: January 1941 to December 1945, at the Rattlesnake Island station. (Some previous data also exist, but are not as complete as the 1941-45 data.)

Measurements of total alkalinity and turbidity were available at Lake Erie filtration plants and from Chandler's investigations for the same time intervals. Since the plant data were monthly averages, Chandler's data were likewise reduced, with all observations for a given calendar month averaged to obtain a monthly mean. Direct comparisons between the onshore and open lake observations could then be attempted. Chandler's observations of total alkalinity were obtained once a week, on the average, so they probably do not present as realistic a mean value as those from the plants which are based on 20 to 30 daily observations. On the other hand, his turbidity observations were made almost daily, except in mid-winter.

Determination of Representativeness.—On the basis of geographical situation, Lorain, Vermilion, Elyria, and Avon Lake appeared to possess the greatest likelihood of being representative stations for the west basin, they being so situated as to sample the effluent of the west basin indicated by the composite surface circulation. Cleveland's location at the region of transition between west and central basin water made it a less strong possibility. Although the east-flowing south shore current appears to transport west basin water past the intakes of Sandusky, Huron, Fairport, Painesville, Ashtabula, Conneaut, and Erie, all but the latter two were eliminated as representative west basin stations for the following reasons:

Sandusky: alkalinity data of plant and data of Lake Erie Pollution Survey (State of Ohio, 1953) indicated intake water as being partially from Sandusky Bay.
Huron: as for Sandusky.
Fairport: local industrial pollution made representativeness of data suspect.
Painesville: as for Fairport.
Ashtabula: raw water alkalinity not measured.

Conneaut and Erie were considered only remote possibilities, due to their great distance from the west basin and the likelihood of their sampling, at least in part, central basin water.

The positioning of the water intake in the lake (discussed later) at Vermilion, Elyria, Avon Lake, and Conneaut strongly suggested that they be removed from further consideration; however, they were retained initially for analysis along with Lorain, Cleveland, and Erie, as discussed below.

Time graphs were constructed on which monthly average total alkalinities and turbidities for each of the plants indicated above were plotted, along with Chandler's Bass Islands data, for comparative purposes.

In the case of total alkalinity, good visual agreement was obtained between Lorain and Chandler, Conneaut and Chandler, Vermilion and Chandler, and Cleveland and Chandler, both as to trends in alkalinity fluctuations and absolute values. Of these, best agreement existed between Lorain and Chandler and Conneaut and Chandler for the years 1938-40. Significant coefficients of correlation were obtained for these latter pairs. For the years 1943-45 (Chandler's Bass Islands data for 1941-42 are not available) there was less agreement between them, and a significant coefficient of correlation was no longer obtained. Visual inspection for these latter years indicated that, of all plants, best agreement existed between Lorain and Chandler.

A time graph was constructed on which were plotted the monthly maximum and minimum values for Lorain and for Chandler. Connecting these points resulted in two "bands" expressing the ranges of total alkalinity observed at the two locations. Overlapping of the two bands occurred in 51 months. Discrepancies in this plot prompted one further comparison. The average ranges of total alkalinity variation for the whole period of observation were computed for both Lorain and Chandler. This gave a single average range for each of the locations. The average range for each location was entered upon a time graph by centering it upon the monthly mean of each month. The two bands thus produced overlapped in 55 of the total 62 months (Fig. 5). This is taken as indicating that, with respect to total alkalinity, *average* conditions observed at Lorain reflect *average* conditions in the Bass Islands.

Before taking up turbidity, a discussion of the good agreement of onshore-offshore alkalinities during 1938-40 versus the poorer agreement during 1943-45

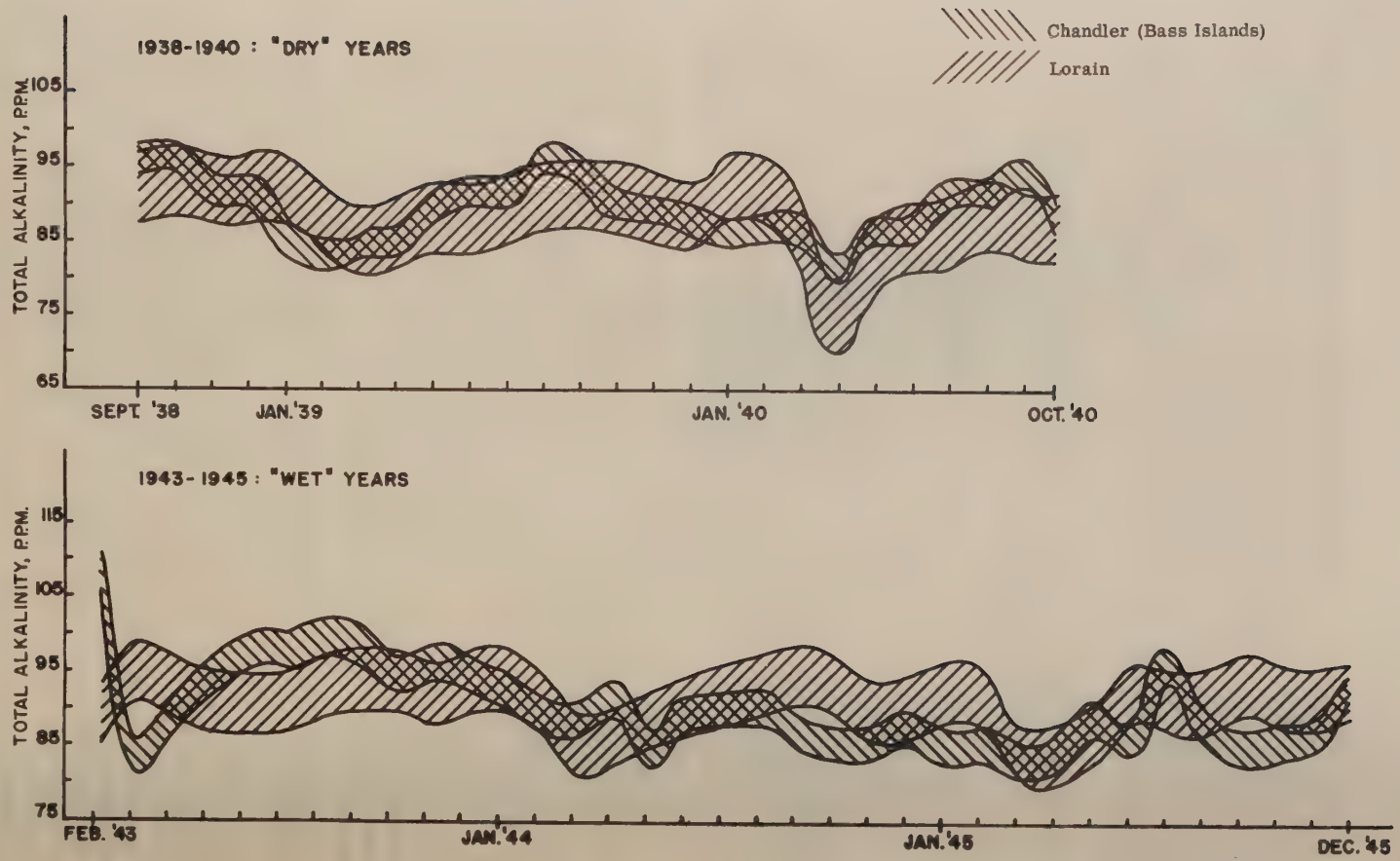

Fig. 5. Comparison of average total alkalinity ranges, Chandler (Bass Islands) and Lorain; 1938-40, 1943-45.

is in order. The various factors considered as possible agents in bringing about the observed disparity are discussed below:

(1) Errors in sampling and determination of alkalinities. There is no basis for suspecting operational error, either at the filtration plants or in Chandler's observations.

(2) Changes of intake location. None of the plants under consideration changed the location of their intakes during 1938-45.

(3) Changes of personnel at filtration plants. No changes occurred.

(4) Prevailing winds. It was thought that significant changes in direction of prevailing winds during 1943-45, as compared to 1938-40, might have resulted in alterations of average current patterns which in turn would have altered the distribution of total alkalinity. As a check on this hypothesis, average monthly wind directions and speeds were obtained for Cleveland from the United States Weather Review. Vector plots were constructed in order to obtain the average wind direction and speed for the two periods under consideration. Although monthly deviations from the average were present, no long-time differences occurred, the average directions being essentially the same for the two periods.

(5) Alkalinity of tributary streams. A number of Ohio streams tributary to Lake Erie were subjected to chemical analysis during 1950-52 as a part of the Lake Erie pollution survey conducted by the State of Ohio Water Resources Commission (State of Ohio, 1953). No direct or consistent relationship between actual alkalinity values of the streams and those concurrently observed at Lorain are apparent, other than the regular seasonal variations generally exhibited by total alkalinity in natural bodies of water.

(6) Runoff. This was the only factor in which there was a significant difference between 1938-40 and 1943-45. Among the gauged streams entering this portion of Lake Erie the Maumee, Sandusky, Cuyahoga, and Ashtabula were selected as indicators of runoff conditions. Using volume-of-flow data from the U. S. Geological Survey Water Supply Papers, the combined annual runoff of these four rivers was obtained by totaling their mean monthly discharges for each of the years 1938-45. Runoff during 1943-45 was about 50% higher than in 1938-40. The increase was general over the entire west-basin region; it included the Detroit River as well as the above rivers. It is thus established that the years of poorer agreement between onshore and offshore alkalinities were years of materially increased runoff.

Turbidity observations obtained by Chandler at Rattlesnake Island between 1941 and 1945 were in generally good agreement with those recorded at Lorain in the same years (Fig. 6). At both locations there are two "pulses" of turbidity per year, one in the spring and the other in the fall. The spring pulse contains higher turbidity values than does the fall. Comparison of these twice-yearly pulses with the runoff of the Black River* at Lorain reveals that the spring pulse occurs at the time of the late-winter-early-spring melt-off. The fall pulses occur during periods of greatly reduced river flows. The spring pulse is probably the result of suspended materials carried into the lake by runoff waters and also, to a less degree, of the spring plankton bloom which regularly occurs at this period. The fall pulse is probably due to bottom sediments suspended by winds and to the fall plankton bloom; the decreased runoff would contribute very little suspended material at this time.

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*The Black River was not gauged; monthly discharge figures for it were obtained from the averages of the Sandusky and Cuyahoga rivers, the nearest gauged streams. The monthly discharge rates per square mile of watershed for these two rivers were averaged and the average per square mile multiplied by the watershed area of the Black.

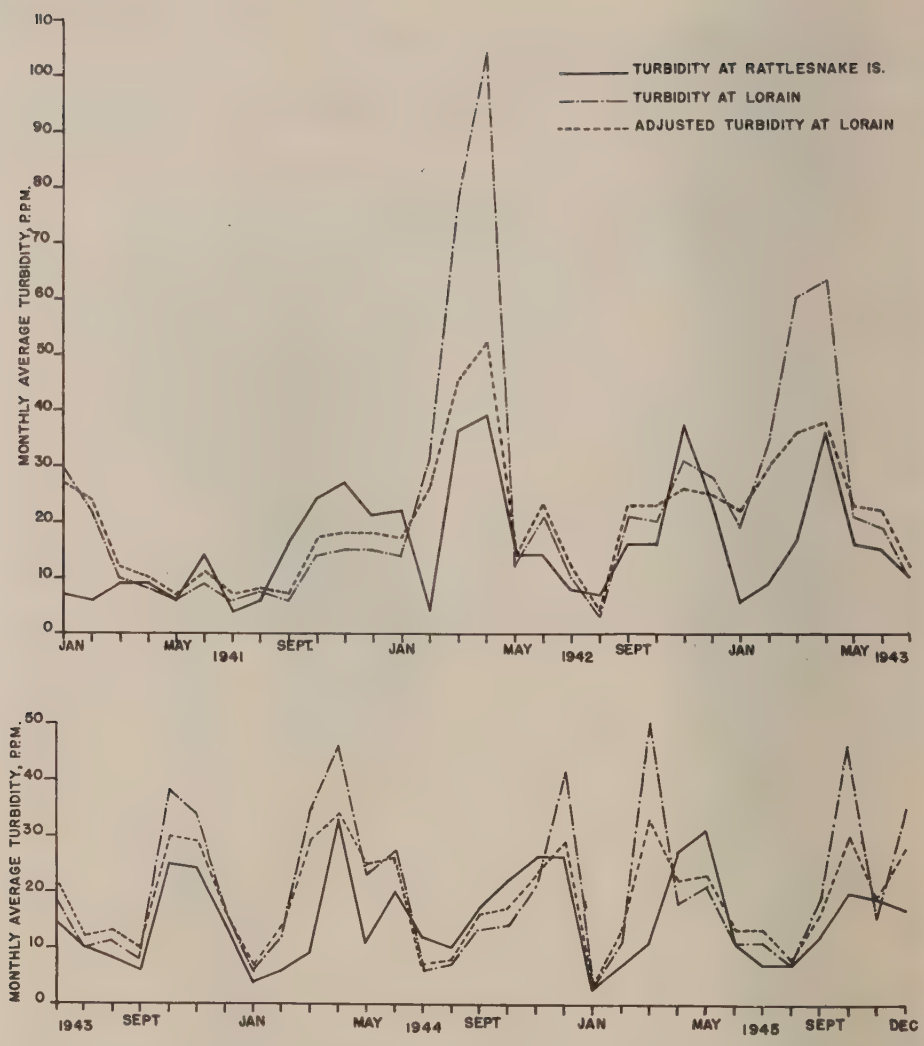

Fig. 6. Temporal variation of turbidity at Rattlesnake Island and Lorain, with adjusted values for Lorain; 1941-45.

In view of the favorable agreement in trends, and of the little difference in actual values, between turbidity observations at Lorain and Rattlesnake Island the possibility of applying corrections to bring the two into even better agreement was considered. A scatter diagram was made in which average monthly values at Lorain were plotted against the difference in monthly means of Chandler and Lorain. This gave a curvilinear arrangement of points to which a curve was fitted by eye (Fig. 7). The curvature and scatter of points increased with decreasing turbidity values.

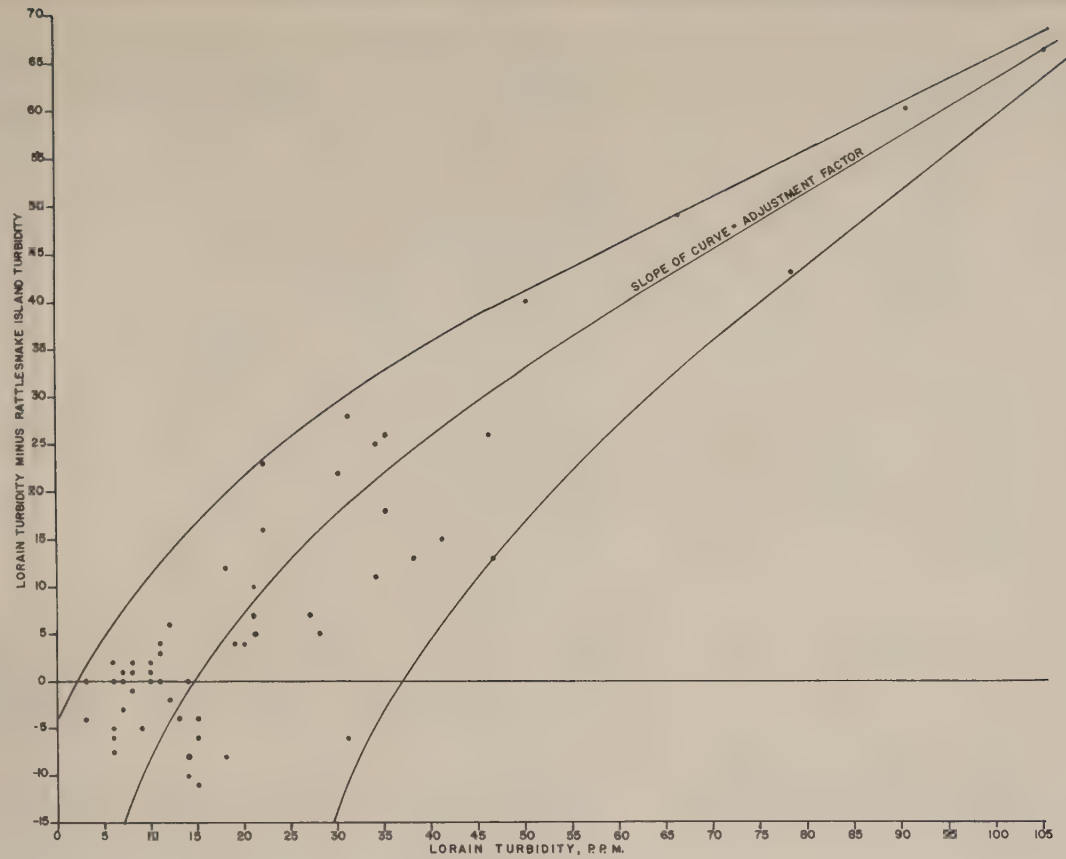

Fig. 7. Adjustment curve, Lorain turbidity to Rattlesnake Island turbidity.

A series of adjustment factors was derived from the slope of the curve by breaking the curve into a series of segments, assuming each segment to be a straight line, and determining the slope of the segment. Adjustment factors were actually computed only for that portion of the curve lying above Lorain turbidities of 20 ppm. Turbidities below this value exhibited such a large scatter as to give unrealistic adjustment factors; an arbitrary factor of 1.20 has been used for this range. It appears to perform satisfactorily. Adjustment factors and the turbidity ranges to which they apply are as follows:

Lorain Turbidity ppm		Adjustment Factor		
0-20	X	1.20	=	Rattlesnake Island turbidity
21-25		1.10		
26-30		0.90		
31-35		0.85		
36-40		0.80		
41-45		0.75		
46-50		0.65		
51-80		0.60		
81-100		0.55		
101-		0.50		

The adjusted values of Lorain's turbidities are shown in Figure 6.

It appears reasonable to conclude, on the basis of total alkalinity and turbidity observations, that physical-chemical data as obtained at the Lorain filtration plant can be considered representative of water flowing through the island region from the west basin. This water, as it arrives at the Lorain intake, appears to be a blend of the various west basin waters (primarily the effluents of the Detroit, Huron, Raisin, Maumee, and Portage Rivers), and so most nearly represents the mixed product of the west basin waters located to the south of Pelee Island. It has been pointed out (page 7) that unmodified Detroit River water passes north of Pelee Island through Pelee Passage. As the Lorain intake obviously does not sample this water, Lorain data are not representative of the northernmost portion of the west basin. This factor must always be carefully considered in utilizing data from the Lorain plant. It must also be remembered that data as obtained at Lorain appear to be more representative of mixed waters from the west basin during seasons of normal or below-normal runoff than during periods of abnormally high runoff. Furthermore, during periods of winds from easterly quarters, the lake circulation may be altered to the extent that Lorain may temporarily fail to sample west basin water.

REPRESENTATIVE STATIONS FOR THE CENTRAL BASIN

Since one of the chief parameters utilized in the selection of representative stations has been total alkalinity, it should at this time be pointed out that in the central basin there is a north-south horizontal gradient of total alkalinity in which values decrease toward the south. This situation is the reverse of that encountered in the west basin, in which lower alkalinity values are found in the north where the Detroit River enters the lake, and higher values in the south where relatively large amounts of admixed Maumee River water occur. The gradient existent in the

central basin is apparently due to the very high alkalinity values found in the tributary streams of the Canadian shore (Thomas, 1954), and to the bedrock formations underlying the lake.

Both the central and east basins are underlain by shale and limestone; in the central basin the limestone is confined to a narrow region roughly parallel to the north shore (Hough, 1958). The remainder of the basin is underlain by shale. The dissolution of limestone by carbon dioxide in the bottom waters near the north shore and the upwelling of these waters along this shore may account in part for the higher total alkalinity values found in the northern portion of the central basin.

The north-south gradient in alkalinity appears in the "Shearwater" data of 1929 (Fig. 4) and the University of Western Ontario data of 1947-53 (Appendix II).

Assessment of representative stations for the central basin was largely on the basis of the 1929 "Shearwater" data, as data obtained by the University of Western Ontario were practically all confined to the northern portion of the basin. Although the data of "Shearwater" Cruise 2 of June, 1929, were the only data suitable for the construction of a circulation pattern, total alkalinity and turbidity data from the remaining three cruises in July, August, and September 1929 were utilized in the analysis of the representativeness of central basin stations. Alkalinity and turbidity observations for all cruises were obtained from surface and bottom only. Cleveland and Erie were considered as the possible south-shore representative stations for this basin, they being the only two which had not been eliminated from consideration on the basis of intake location, pollution effects, or some other factor.

From circulation evidences, as well as geographic location, it appeared that Erie possessed better qualifications than Cleveland for the position of representative station for the central basin. The Erie intakes (there are two plants, with intakes close to each other) appeared to be in such a position as to sample an integrated product of the easterly south shore current and the cross lake current from Long Point. The surface current pattern indicates that water from both these sources might be brought past the Erie intakes. Cleveland, on the other hand, is so far west as to be sampling predominantly the water of the easterly south shore current only, and further, analysis of the circulation suggests that the Cleveland intakes may at times sample water which is predominantly an unmodified effluent of the west basin.

From "Shearwater" Cruise 2 were available total alkalinities, turbidities, and water temperatures which could be used in analyzing the representativeness of Cleveland and Erie. It is obvious that as complete an analysis could not be performed here as with Chandler vs. Lorain, where data for the west basin were available over a period of years.

Total alkalinity and turbidity observations obtained at Cleveland's Division and Baldwin filtration plants in 1929 were compared with values of these parameters at "Shearwater" stations 47 and 48. These stations were located 2 and 14 miles, respectively, north-northwest of the two plant intakes, and the depths at the stations were fairly comparable to the intake depths. The depth of the Baldwin intake is 28 feet and that of the Division intake 36 feet; station 47 was located in 38 feet of water and station 48 in 44 feet. The comparisons of the two filtration plants with data from stations 47 and 48, for each of the four cruises, are summarized in Table II.

In the case of total alkalinity, best agreement is between the Division plant and the average of the bottom values as observed at the stations.

The best agreement of turbidity values lay between the Baldwin plant and the average bottom values of the two stations.

In summary, the total alkalinity and turbidity data as obtained by the two Cleveland filtration plants are, to a fair degree, representative of these two

Table II. Comparison of Data of the Division and Baldwin Filtration Plants, Cleveland, with Data of "Shearwater" Stations 47 and 48

All data are for 1929

	Division	Baldwin	Average of Stations 47 and 48		
			Surface	Bottom	Surface and Bottom
Alkalinity (ppm)					
June	93	92	97	93	95
July	93	92	96.5	94	95
Aug.	95	93	95.5	95	95
Sept.	96	94	97.5	98.5	98
Turbidity (ppm)					
June	25	8	12	16	14
July	13	6	4	8	6
Aug.	13	6	7	8	7.5
Sept.*	16	7	10	10	10

*Station 47 only.

parameters as they occur somewhat farther out in the lake. Evidence from the circulation pattern of the lake, however, indicates that Cleveland is sampling water from the extreme western portion of the central basin, and may frequently sample relatively unmodified west basin water. The strong turbidity gradient along the south shore in the vicinity of Lorain and Cleveland as observed by "Shearwater" Cruise 2 (Fig. 3) is indicative of the presence of west-basin water.

At Erie, observations of total alkalinity, turbidity, and water temperature as obtained at the Chestnut Street filtration plant in 1929 were compared with values of these parameters as obtained by "Shearwater" Cruise 2 (Erie's west filtration plant did not become operative until 1932). Comparisons were made in two ways: first, all "Shearwater" stations in the central basin, including those to a distance five miles east of Erie, were combined to obtain mean values of total alkalinity and turbidity for surface, bottom, and average of surface and bottom. This was done for each of the cruises, that is, June, July, August, and September. Secondly, stations 37, 38, 47, and 48 were similarly combined to obtain average values for each of the cruise months. These stations lay, respectively, three miles north of Ashtabula, 3 miles north of Fairport, and 2 and 14 miles NNW of Lorain. They were indicated by the circulation pattern as lying within the eastward south-shore current which passes the Erie intakes; and were compared, separately from all the central-basin stations, with the Erie data in an effort to determine whether Erie might be more representative of this water than of the central basin as a whole. Stations 37, 38, 47, and 48 will hereafter be referred to as "selected stations." Temperature data from the "Shearwater" cruises were treated similarly to alkalinity and turbidity, with the following two exceptions: (1) Temperature was obtained at each station at surface, 10 meters, and bottom. Only the surface and 10-meter observations were compared to the Erie values, since these were nearer the intake level of the plants and gave a more realistic test of Erie's representativeness.

(2) In addition to data from the June, July, August, and September cruises, temperature data from a May, 1929, cruise were available and used, although alkalinity and turbidity data for this cruise were lacking.

Comparisons of averaged "Shearwater" data and monthly average data of the Chestnut Street plant are summarized in Tables III and IV.

It may be seen from Table III that, compared to the average of all stations, alkalinities observed at Erie are consistently low, by 4 to 7.5 parts per million. Erie's values agree best with the bottom values of the selected stations, which were located within the south shore current. On the basis of total alkalinity, then, the Erie intakes appear to sample predominantly water from the south shore current, rather than a well integrated product of water from the entire central basin. Erie plus 3 ppm would appear to give a working estimate of selected-station alkalinities under most conditions.

That Erie is not representative of the northern and western parts of the central basin is shown by a comparison of total alkalinity data at Erie with data obtained at University of Western Ontario stations 2, 3, 4, and 5. These stations were situated 6, 14, 20, and 26 miles south of Point aux Pins. Alkalinity values at Erie were as much as 28 ppm below those observed at UWO stations, and only at one time were the Erie values less than 11 ppm below the station values. The existence of a decreasing north-south horizontal gradient of total alkalinity in the central basin has been discussed above and is reflected in these two sets of data.

Turbidity values observed at Erie are consistently and irregularly higher than those of the open lake as indicated by the "Shearwater" data. This is true for both "all stations" and "selected stations." It is likely that turbidity at Erie is influenced locally by the sediment-suspending effects of wind and/or current action.

From Table IV, it may be seen that agreement of intake temperatures at Erie with those observed by the "Shearwater" is excellent. Erie's values agreed more closely with surface temperatures than with 10-meter temperatures, correlation of Erie with the selected stations is a little better than with the entire basin, but the difference is slight. It should be noted that agreement was least good in May, when the intake water was warmer than that of the open lake. This is to be expected, since this corresponds with the season of spring warming, when nearshore waters would have attained a higher temperature than those farther offshore.

Comparisons of intake temperatures at Erie also were made with surface temperatures (both in centigrade) observed at University of Western Ontario stations 2, 3, 4, and 5. They are summarized in Table V.

Agreement of Erie intake temperatures with those at UWO stations is, for the most part, quite good. Once again, the effects of along-shore warming in the spring are indicated in the one set of April temperatures, where the water at Erie was nearly twice as warm as that in the open lake. More rapid autumnal cooling of the shallow onshore water is shown in the September and October data of 1949 and 1950.

It must be remembered, as has already been pointed out, that strict comparability between observations obtained at Erie and those from the open lake cannot be implied, since it has been necessary to compare monthly averages based on a relatively large volume of data at Erie with either single days' observations, or averages based on no more than four observations, from the open lake. Considering the paucity of open lake data available, the comparability that has been obtained must be considered very good.

With respect to total alkalinity, Erie must be considered a good representative station for only the southern half of the central basin. In regard to surface water temperatures, however, those observed at Erie do not differ materially

Table III. Comparison of Alkalinity and Turbidity Data of the Chestnut Street Filtration Plant, Erie, Pa., with Data of "Shearwater" Stations. ("Selected stations" are those located in the eastward south-shore current.)

All data are for 1929

	All Stations			Selected Stations			Erie
	Surface	Bottom	Surface and Bottom	Surface	Bottom	Surface and Bottom	
Alkalinity (ppm)							
June	99	97.5	98	95	94	95	92
July	101	98	99.5	96	95	95	92
Aug.	97	96.5	97	97	95.5	96	93
Sept.	98	98	98	97.5	99	98	93
Turbidity (ppm)							
June	4	6	5	9	11	10	12
July	3	6	5	5	6	5	10
Aug.	2	5	4	5	6	6	16
Sept.	4	5.5	5	7	7	7	20

Table IV. Comparison of Temperature Data of the Chestnut Street Filtration Plant, Erie, Pa., With Data of "Shearwater" Stations. ("Selected stations" as for Table III.)

All data are for 1929

Month	Temperature, °C				Erie
	All Stations		Selected Stations		
	Surface	10 Meters	Surface	10 Meters	
May	8.4	6.6	9.8	7.8	11.7
June	17.6	13.2	18.0	14.5	17.4
July	20.2	17.7	21.6	19.1	21.6
Aug.	20.9	20.0	21.4	20.7	21.8
Sept.	19.4	19.4	19.7	19.6	20.3

Table V. Comparison of Temperature Data of the Chestnut Street Filtration Plant, Erie, Pa., with Surface Temperature Data of University of Western Ontario Stations 2, 3, 4, 5

	1947		1948		1949		1950		1951	
	Erie	UWO	Erie	UWO	Erie	UWO	Erie	UWO	Erie	UWO
April			8.2	4.5						
May							9.6	11.9	11.2	11.5
June			16.5	16.0	18.4	19.6*	16.8	16.9	15.7	18.6
July	18.8	22.1*	20.2	20.3	20.1	24.4*	20.3	20.8	21.6	22.9
Aug.	22.2	25.7	22.7	23.5*	24.3	24.2	22.5	21.9*	22.8	23.2
Sept.	22.3	18.6			18.6	19.9	17.9	22.4*		
Oct.							16.2	19.4*		

*Based on single observation from station 2.

from those of the entire basin. This apparent discrepancy is resolved when one considers that surface temperatures throughout the basin are controlled by very nearly the same climatic regimen and should not exhibit too much variability, except in regions of upwelling. One appears to be justified, then, in accepting the intake temperatures at Erie as being representative, within a few degrees, of the surface temperatures existing anywhere within the central basin. The strongest exception to this representativeness would be in comparing Erie's temperatures with those along the north shore, where the existence of the counterclockwise eddies appears to result in upwelling of cooler subsurface water, the temperatures of which would not be typical of surface temperatures over most of the basin.

Since Erie can be considered, with respect to total alkalinity and turbidity, representative of only the southern half of the central basin, conditions obtaining in the basin as a whole could be more accurately depicted if there were two representative stations, one on the south shore (satisfied by Erie), and one on the north. Although a number of municipalities in the province of Ontario possess filtration plants which obtain water from Lake Erie, none of these make routine physical-chemical analyses of lake water as far as this investigation has been able to determine. Analyses of intake water at Port Stanley, made by the Industrial Minerals Division, Mines Branch, Canada Department of Mines and Technical Surveys (Thomas, 1954) indicate a degree of comparability between this water and that sampled by UWO stations 2, 3, 4, and 5. Intake water at Port Stanley was subjected to complete analysis once monthly from February 1948 to February 1949. During this period the UWO stations were visited during June, July, August, and September. The average total alkalinity for the four samples obtained during these months at Port Stanley was 100 ppm; the average from all depths at the UWO stations was 106 ppm. Considering once again the scanty data available for comparison, this is good agreement. Centigrade temperature data from the two sources were compared on a month-to-month basis:

	April	May	June	July	August	Sept.
University of Western Ontario	4.2	-	12.7	16.3	20.3	21.6
Port Stanley	0.6	3.3	4.4	15.6	18.3	15.6

The notable tendency of the Port Stanley temperatures to remain consistently below those as observed at the open-lake stations is probably due to upwelling occurring near the north shore in the Port Stanley vicinity, caused by the previously mentioned eddy occurring here. The proximity of Port Stanley to this upwelling makes its value as a representative station questionable, since it would at different times be effectively sampling different depths. Hence, variability in observations would have to be assessed partially on an unknown basis of effective sampling depth.

The deduced pattern of surface circulation indicates the possibility of Port Burwell as a better location for a north shore representative station, since it lies at the extreme eastern end of the eddy, and near the area of strong onshore current shown by the FWS drift bottle returns.

REPRESENTATIVE STATIONS FOR THE EAST BASIN

The only station in the east basin which could be checked for representativeness was the Erie County (New York) Water Authority filtration plant at Woodlawn, N. Y. The Niagara-Mohawk power station at Dunkirk, N. Y., obtains physical-chemical data, but its records are available for only a few years. Likewise, the U. S. Public Health Service National Water Quality Network Station at the Buffalo municipal water plant has, since October 1957, made various chemical, physical, and biological analyses on an average of two to four times monthly. There are at present no simultaneous open-lake data with which to evaluate these two stations. Because Woodlawn has obvious weaknesses (discussed below), the possible representativeness of Buffalo should receive attention as soon as pertinent open-lake data are available.

Data of 1929 from the Woodlawn plant were compared with open-lake data obtained by the "Shearwater" in the east basin in 1929 (1928 data are also available from previous "Shearwater" cruises, but data from Woodlawn do not include that year). Comparisons were made of total alkalinity, turbidity, and temperature. The procedure was similar to that used for Erie, in that data from Woodlawn were compared with monthly averages of observations from the entire east basin, and also with certain "selected" stations which, according to the deduced circulation pattern, lay upcurrent from the plant's intake. The latter stations were all near the south shore, extending from just off Woodlawn to about the Pennsylvania-New York state line. Results are summarized in Tables VI and VII.

Total alkalinity as observed at Woodlawn is consistently lower than open-lake observations for the east basin. The tabulations of Table VI indicate that this is true for both "all stations" and "selected stations," except for September, when the average value at Woodlawn for that month closely approximated open-lake values.

Average monthly values of turbidity at Woodlawn (Table VI) agreed well with those from the "selected stations," and, for the most part, fairly well with those from all stations in the east basin. The only notable discrepancy is in September, when local disturbances (probably winds) apparently resulted in higher turbidities in the vicinity of the intake.

Temperature observations from Woodlawn (Table VII) do not agree as well with open-lake data as do the plant data at Erie. This may be largely due to the plant's being located on the extreme east end of the lake, where the intake is exposed to the full effect of the internal seiche, the magnitude of which can be quite large. This might explain the lower temperature at Woodlawn for September, when the average of 15°C corresponded closely to the average of bottom temperatures for all stations, whereas in June, July, and August intake temperatures corresponded

Table VI. Comparison of Alkalinity and Turbidity Data of the Woodlawn, N. Y., Filtration Plant with Data of "Shearwater" Stations. ("Selected stations" are those lying upcurrent from the intake as far as the Pennsylvania-New York line.)

All data are for 1929

	All Stations			Selected Stations			Woodlawn
	Surface	Bottom	Surface and Bottom	Surface	Bottom	Surface and Bottom	
Alkalinity (ppm)							
June	100	98	99.5	96	95	96	93
July	99	98	99	98	97	97.5	90
Aug.	98	97	97.5	98	97	97	91
Sept.	98.5	98.5	98	97	97	98	99
Turbidity (ppm)							
June	13	16	14	14.5	15	15	13
July	6	20	13	8	9	8	7
Aug.	4.5	13	9	6	7	6.5	8
Sept.	0.5	8	4.5	0.6	1	1	13

Table VII. Comparison of Temperature Data of the Woodlawn, N. Y., Filtration Plant with Data of "Shearwater" Stations. ("Selected stations" as for Table VI.)

All data are for 1929

Month	Temperature, °C						
	All Stations			Selected Stations			Woodlawn
	Surface	10 Meters	Bottom	Surface	10 Meters	Bottom	
June	13	11	8	12	---	12	17
July	19	17	12	20	---	18	20
Aug.	20	18	14	21	---	20	18
Sept.	21	20	16	21	---	20	15

more closely to average surface temperatures for both "all stations" and "selected stations."

LAKE ERIE REPRESENTATIVE STATIONS: A SUMMARY

It has been shown that for each of the three basins of Lake Erie, a filtration plant exists whose lake water data correlate sufficiently well with open-lake data to justify their designation as the most representative stations for their particular basins. Lorain, Ohio, and Erie, Pennsylvania, chosen as representative stations for the west and central basins, respectively, appear to be more reliable than Woodlawn, New York, the one evaluatable station for the east basin. Waste effluents from steel mills and seiche activity may affect the representativeness of alkalinity and temperature data at Woodlawn. The intakes at Lorain and at Erie appear to be relatively free from the effects of local pollution and seiches, and it is believed that data obtained at these two plants are sufficiently indicative of open-lake conditions to permit their application to practical limnological problems, particularly in regard to the assessment of long-term physical-chemical conditions in the lake.

When and if Erie and Woodlawn are seriously used in watching the trends within the lake, their actual degree of representativeness should be more definitively determined by more offshore cruises. Scarcity of offshore data has been a serious limiting factor in their assessment. Niagara-Mohawk at Dunkirk, New York, and/or the U.S.P.H.S. Station at Buffalo may be better representative stations for the east basin and should be evaluated as soon as possible.

A REPRESENTATIVE STATION FOR LAKE MICHIGAN

Through the kindness of Mr. Russell L. Johnson, Engineer in Charge, Northern Peninsula Office, Michigan Department of Health, we are able to indicate a representative water plant on Lake Michigan. In collating local wind and circulation near Muskegon, Michigan, (as indicated by Ayers *et al.* 1958) with raw water temperatures from the recording thermometer at the Muskegon water plant, Mr. Johnson has very clearly shown that under different winds Muskegon samples both surface water from about 20 miles out in the lake and subthermocline water from the region outside Muskegon.

His studies (personal communications) show that under south, southwest, or west winds, surface waters from the open lake approach Muskegon. On the second day of winds from these directions notable rises in water temperature occur, and by the fourth day of such winds isotherms originally about 20 miles offshore are present at the intake. Referring to Figure 4 of the Lake Michigan paper (Ayers *et al.*, op. cit.), Mr. Johnson says, "Figure 4 shows that, on June 28, the 17° isotherm for the surface water was located several miles offshore at Muskegon. On June 29, according to Figure 15, this isotherm had reached shore in this part of the lake. At intake level off Muskegon, the water temperature started rising at about 0100 hours on June 29, the day of Synoptic Cruise V. It reached 17°C (62.6°F) late in the day on June 30 or early on July 1." Winds at Muskegon were from the south for six days beginning on June 27.

His studies also show that the atypical east-shore south current observed in Lake Michigan on August 9 and 10, 1955, in Synoptic Cruises VI and VII probably began on August 7. On that day the water temperature at Muskegon began a sharp decline which lasted through August 9. During the sharp decline, temperature fell from 80.0°F (26.6°C) to 45.0°F (7.2°C) between 0630 of the 7th and 0430 of the 9th. Figures 5, 16, 28, and 41 of the Lake Michigan paper all show 7.2° water to be

subthermocline water. This temperature break accompanied north winds and east winds (offshore winds) that began on August 7 and continued for at least five days.

Mr. Johnson's studies also indicate that northwest winds cause strong upwelling at Muskegon.

It appears reasonable to believe that Muskegon on the fourth day of winds from the south, southwest or west is sampling surface water from about 20 miles (estimated) offshore. It also is reasonable to believe that Muskegon on the third day of winds from the northwest, north, northeast, or east is pumping subthermocline water representative of the hypolimnion of the deep basin outside Muskegon.

EFFECT OF INTAKE LOCATION UPON VARIABILITY OF DATA

While the studies pertaining to selection of representative stations were going on, it was noted that there was an apparent relationship between intake location and temporal variability of observed alkalinity and turbidity at a given plant.

To examine the effects of intake location, five plants were chosen whose intakes were located at different distances from shore. The plants and their intake locations are:

Filtration Plant	Intake Distance from Shore (ft)	Intake Depth (ft)
Cleveland (Division Plant), Ohio	21,120	36
Erie, Pennsylvania	6,200	22
Lorain, Ohio	2,000	13
Avon Lake, Ohio	1,400	12
Fairport, Ohio	1,000	12

It will be noted that beyond the distance of 1,400 feet from shore (at Avon Lake), increasing distance from shore resulted in increasing intake depth.

For these five plants, data of the twelve-year period 1940-1951 inclusive were arbitrarily chosen as representing average conditions. For each year's data at each plant the lowest monthly average, of both turbidity and alkalinity, was subtracted from the highest monthly average to obtain the average range for the year. The twelve annual ranges thus obtained for each plant were combined to give a twelve years' overall average range for each parameter at each plant. These values were then entered upon graphs in which ranges of turbidity and alkalinity were plotted against distance of intake from shore and against depth of intake.

The turbidity results were quite clear-cut (Fig. 8). Variabilities were about the same at Cleveland and Erie, with Erie showing slightly less variability. This is apparently due to the geographic position of the Cleveland intakes. They are situated where they may be reached by waters of both the western and central basins. The Cleveland variability was most probably increased by alternate sampling of western and central basin waters as shifts in wind direction bring one or the other of these two water masses over the intakes. Variability increased sharply at Lorain where the intake is 2,000 feet out, and was still more pronounced at Avon Lake and Fairport whose intakes are 1,400 and 1,000 feet from shore respectively.

Variation of total alkalinity with intake location (Fig. 9) described a curve approximating that for turbidity. Cleveland again had a greater range of variability than did Erie (and the same reason apparently applied). Lorain had a slightly higher variability than Fairport but the difference, half a part per million, was probably not significant.

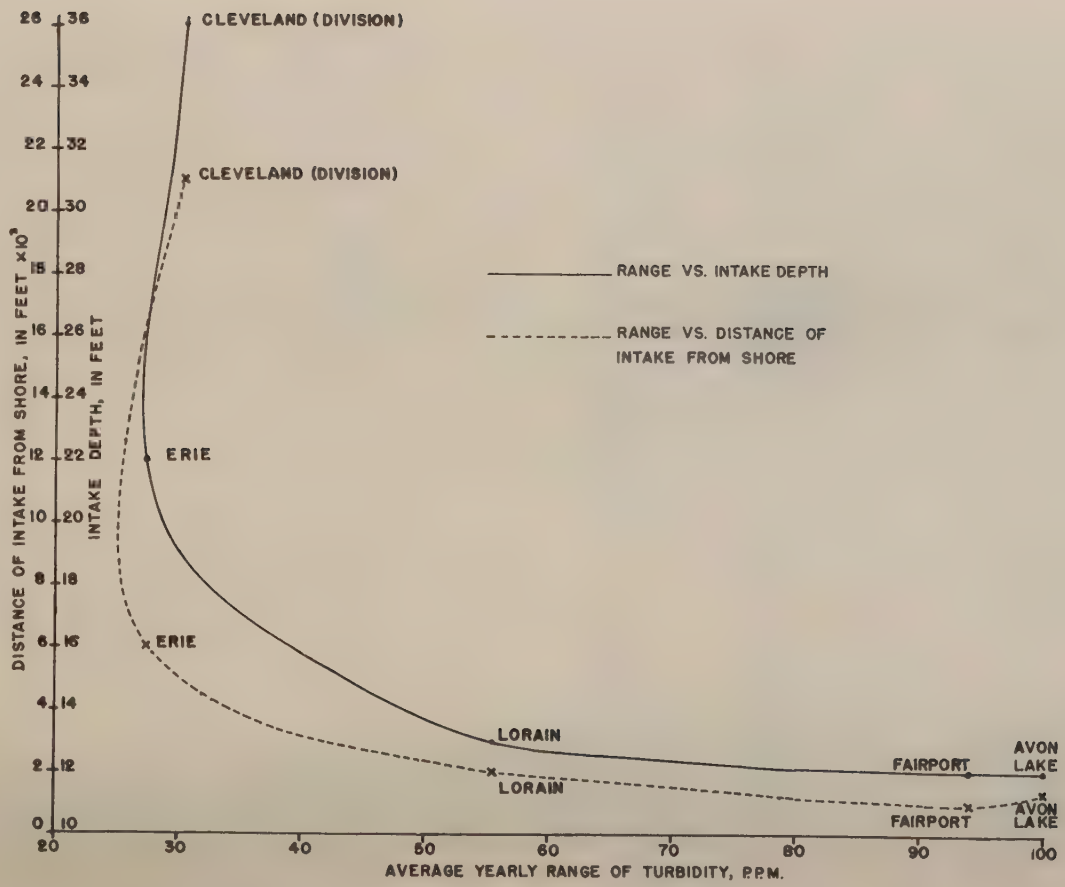

Fig. 8. Average yearly range of turbidity vs. distance from shore and depth of intake, at Cleveland, Erie, Lorain, Fairport and Avon Lake.

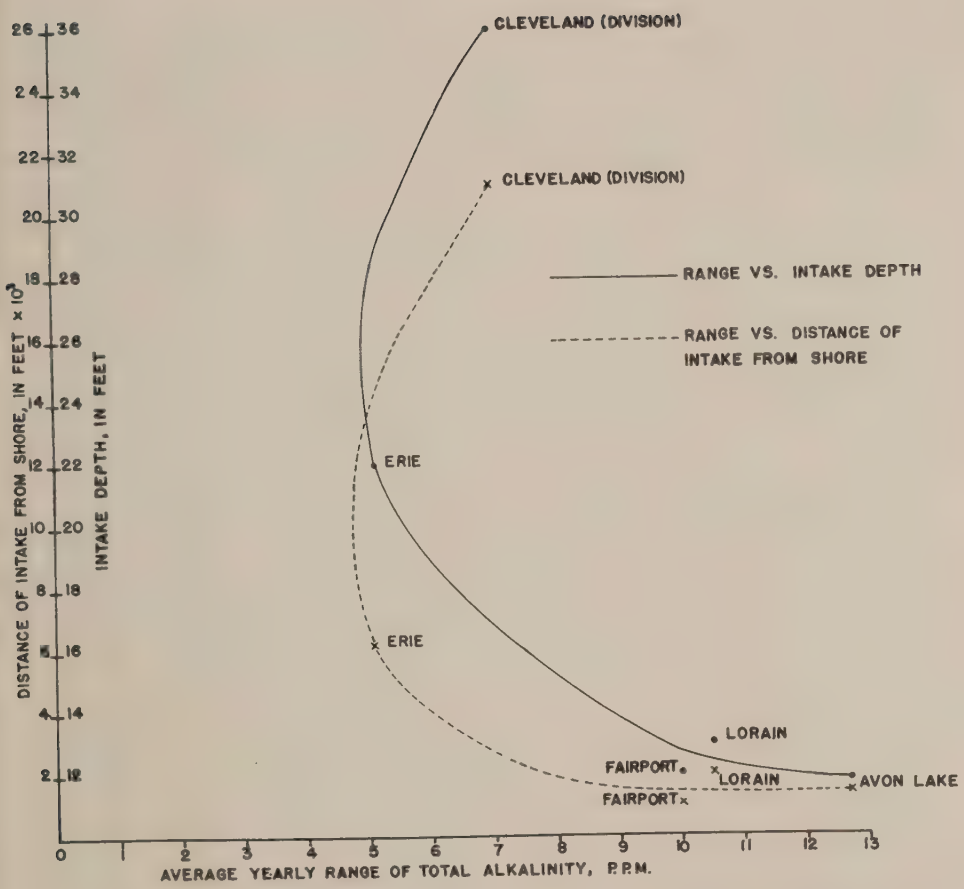

Fig. 9. Average yearly range of total alkalinity vs. distance from shore and depth of intake, at Cleveland, Erie, Lorain, Fairport, and Avon Lake.

The curves relating variability to intake depth approximated the distance-from-shore curves and both showed lessened variability with greater depth and with greater distance from shore. This is to be expected since distance from shore and depth of intake are not mutually independent variables.

Further evidence of the effect of intake location has come from the data of the Conneaut plant, whose intake was moved farther out from shore in 1933. The previous location has not been ascertainable, but it was inshore of the present site. Variability of total alkalinity before and after the change is depicted in Figure 10 (complete data for 1932 and 1934 were not available). The bars are yearly ranges of alkalinity, based on monthly averages, for the years 1923 through 1942. The stabilizing effect of the intake change is evident. The *greatest* range occurring after 1933 (26 ppm in 1940) is equal to the *least* range that occurred in the years prior to the change (26 ppm in 1928).

It seems likely that distance of intake from shore is a more important variable than intake depth. Best correlation of alkalinity and turbidity data from Lorain

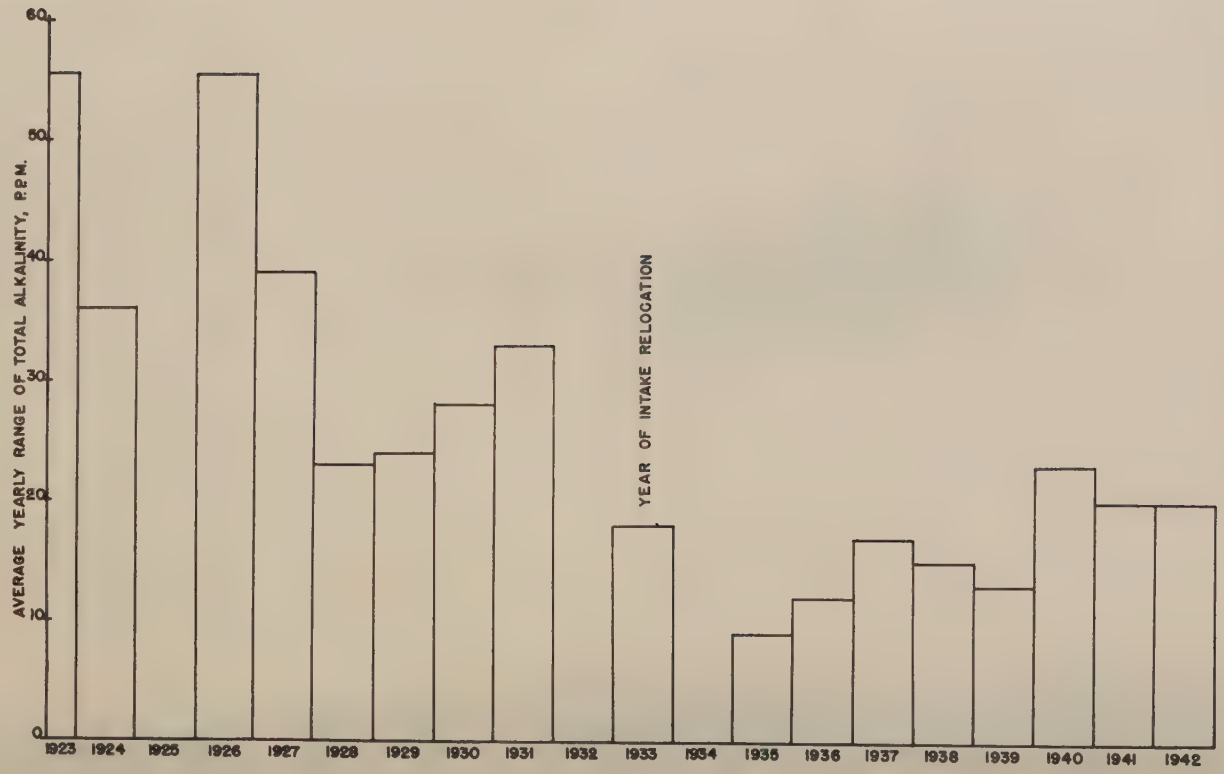

Fig. 10. Average yearly ranges of total alkalinity before and after change of intake location at Conneaut.

with those of Chandler from the Bass Islands (discussed later) was obtained in years when rainfall and runoff were normal or below normal, with correlation becoming weak in wet years. If depth of intake were the more important, the reverse situation might have been expected, i.e., better correlation in wet years when lake level might be rising and depths to the intakes increasing (assuming deeper waters to exhibit smaller fluctuations in physical-chemical parameters). But during 1938-40, when the best correlation was obtained, the lake level was significantly lower than in 1943-45.

There appears to be a critical distance, about 2,000-4,000 feet offshore, at which a marked change in variability of parameters occurs. At greater intake lengths, fluctuations are small. At less than this critical range, decreasing distance from shore is accompanied by increasing fluctuation. It appears, also, that increased runoff from tributary streams during wet years serves to increase alongshore variation in the several parameters, and those plants with intakes farthest from shore are least affected. During dry years the plants with short intakes reflect, in the decreased variability of their data, the decreased alongshore fluctuations that accompany decreased runoff.

The above must not be taken to imply that depth of intake is unimportant in all respects. For drinking-water purposes, it is desirable that the intake be, if possible, below the normal depth of the thermocline. The scanty data presently available (not discussed in this report) indicate that water of materially better quality is to be had from beneath the thermocline. The reason for this appears to be that the density stratification accompanying the thermocline confines to the epilimnion much of the pollution introduced along shore.

Height of intake above bottom appears to be an independent secondary factor that is imposed upon the effect of distance from shore and depth below surface. The two intakes at Cleveland are located the same distance from shore, but that for the Baldwin plant is higher off the bottom than is that of the Division plant. The raw water of the Baldwin plant consistently runs 7 to 17 ppm lower in turbidity and 1 to 2 ppm lower in alkalinity than does that of the Division plant (see Table II). The reason for the differences appears to be that sediments resuspended from the lake bottom by winds or currents have freer access to the lower intake of the Division plant. In the selection of a representative station, then, with all other considerations being equal, priority should be given that plant whose intake is located the greatest distance off bottom.

A TECHNIQUE FOR DETERMINATION OF WIND PATTERN OVER A LAKE

Basic to the study of properties of a large body of water is knowledge of its currents. The distribution of water properties such as alkalinity and turbidity is influenced by the movement of lake currents. Current variations are brought about by two principal factors, 1) temperature distribution in the water and 2) wind at the air-water interface.

The techniques of dynamic height determination derived from considerations of the density distribution in water, in order to compute water currents, are well known in oceanography and have been used with success in previous studies of some of the Great Lakes (Ayers, *et al.*, 1956, 1958; Ruschmeyer, *et al.*, 1956; Ruschmeyer and Olson, 1958). The dynamic height method yields an integrated depiction of temperature effect and the wind-distributed field of density. In this depiction the temperature factor is semi-conservative and varies at a relatively slow rate, while the wind factor varies on a day-to-day basis. The wind pattern over a lake, then, is the dominant factor in the pattern of water currents in the lake.

For large bodies of water that are relatively shallow, such as Lake Erie, currents are much more rapidly changed than in deeper lakes of comparable area. This is because shallow water does not represent as great a momentum sink as does deep water. It has been found that current patterns in western Lake Erie, for example, are variable, and frequently vary on an intra-diurnal time scale (FWS M/V *Cisco* Cruise Report III, Ayers, 1958). There is also evidence elsewhere (Saginaw Bay, Johnson, 1958) to indicate the wind-produced changes in shallow water movement may take place with as little as two hours subjection to a new wind regime. It is important, therefore, that the wind field be determined as accurately and frequently as possible.

A technique of kinematic analysis of the atmosphere, known as the streamline wind analysis method, makes possible an accurate computation of the wind-produced currents which affect the distribution and transport of variables that make up the water quality (e.g., alkalinity, turbidity, chemistry). It is also a valuable means for reconstructing the wind regime and current patterns in the Great Lakes at any time during the past 60 years. It is, therefore, both a climatological and synoptic aid in water current analysis. The technique utilizes reports of the wind vector from many observers taken simultaneously; hence analyses made from these data are truly synoptic.

The frequency of reports (and hence possible analyses) is a function of their history. Before the onset of World War II, the frequency of reporting was once per day. After the close of the war, reports became available on an hourly basis. Data density has increased in like manner. For example, in 1899 there were four stations surrounding Lake Erie that reported wind data once per day. At present the number of stations which surround western Lake Erie alone number 21, all of which make hourly reports of most meteorological variables including the wind vector. Some wind records of this group are autographic. In addition to the hourly stations, Powers *et al.* (1959) have shown that there are ten Coast Guard stations around the western basin of Lake Erie reporting the wind vector at either 4- or 6-hourly intervals. On a once-per-day basis there are an additional five water plants that surround the same area of Lake Erie that report the wind vector. Finally, there is a variable number of lake vessels that are equipped with anemovanes which report periodically when operating more than 4 miles from shore. Not counting the vessels, there are three dozen sources for wind data over the

western basin of Lake Erie alone—a ten-fold increase in data density since the turn of the century. The hourly wind reporting stations in the vicinity of all the Great Lakes which are available at present are represented by the station circles shown in Figure 11. Each station reports all meteorological variables including the wind vector.

The basic difficulty in making a wind analysis is not just a function of the data density, but primarily is dependent on the fact that the wind is a vector quantity. It is possible to draw charts and graphs of vector quantities, but it is difficult for the analyst to account graphically for the variation of the vector by one system of lines or isopleths. It is simpler and more accurate to analyze the vector in terms of its two scalar components, speed and direction, by preparing a graph of each scalar separately.

Figure 11 shows the first step necessary in preparing an accurate analysis of the wind direction field. The two digits above the station circle are the reported wind direction in tens of degrees reckoned clockwise from north (36), calm being code 00. The wind data shown are those actually recorded at 1300 EST, 23 October 1958.

With a field of numerical values at hand to express the wind directions, equal-valued lines (isogons) may be constructed. The purpose of the isogons is two-fold. First they give continuous representation of the wind direction field. That is, everywhere along any one isogon the wind direction is the same. The isogons also provide interpolated information of the wind direction between stations. In Figure 11, the isogons are labeled by letter abbreviations, NE, SW, etc.

It is difficult to draw, directly, the streamlines which depict the wind direction field because of the lack of information between stations. Only a crude first approximation to direction field is possible by the direct approach. First, direction arrows must be constructed at each station to show the wind direction graphically. Then streamlines may be drawn, but with confidence only if the data density is high. In only a few locations of the United States (viz., around the major metropolitan centers) is the station coverage dense enough to approximate the detail possible from an isogon analysis. In the interests of accuracy, therefore, the isogon procedure is recommended because it multiplies the density of the data field.

The second step in preparing the streamline analysis is to construct short line segments across each isogon. Each line segment is oriented according to the wind direction of its isogon. That is to say, all line segments on the "north" and "south" isogons, for example, are drawn parallel to the local meridians no matter how the isogon itself varies across the chart; all segments on NW and SE isogons point in these directions; etc. The number of segments drawn is completely arbitrary.

What has been accomplished by the procedure so far described, and illustrated in Figure 11, is to give the analyst a chart composed of as many "wind observations" as he desires. Instead of being restricted to wind data reported by the stations alone, he now has a limitless number of wind directions by which to construct streamlines to show the air-flow at a given moment. In actual practice, isogon intervals of 30 to 45 degrees (those of Figure 11 have an interval of 45°) with line segments one or two latitude degrees apart is a sufficiently detailed field of data from which to draw streamlines.

The third step in the procedure is illustrated in Figure 12. For simplicity, only the line segments from Figure 11 are reproduced. The pattern of air flow is shown by the solid streamlines which are constructed so as to be everywhere parallel to the line segments. This is the only requisite on the construction of streamlines; the speed of the wind is not involved in this analysis. Streamlines can fork and join, but only asymptotically. Exceptions are at singular points where the wind

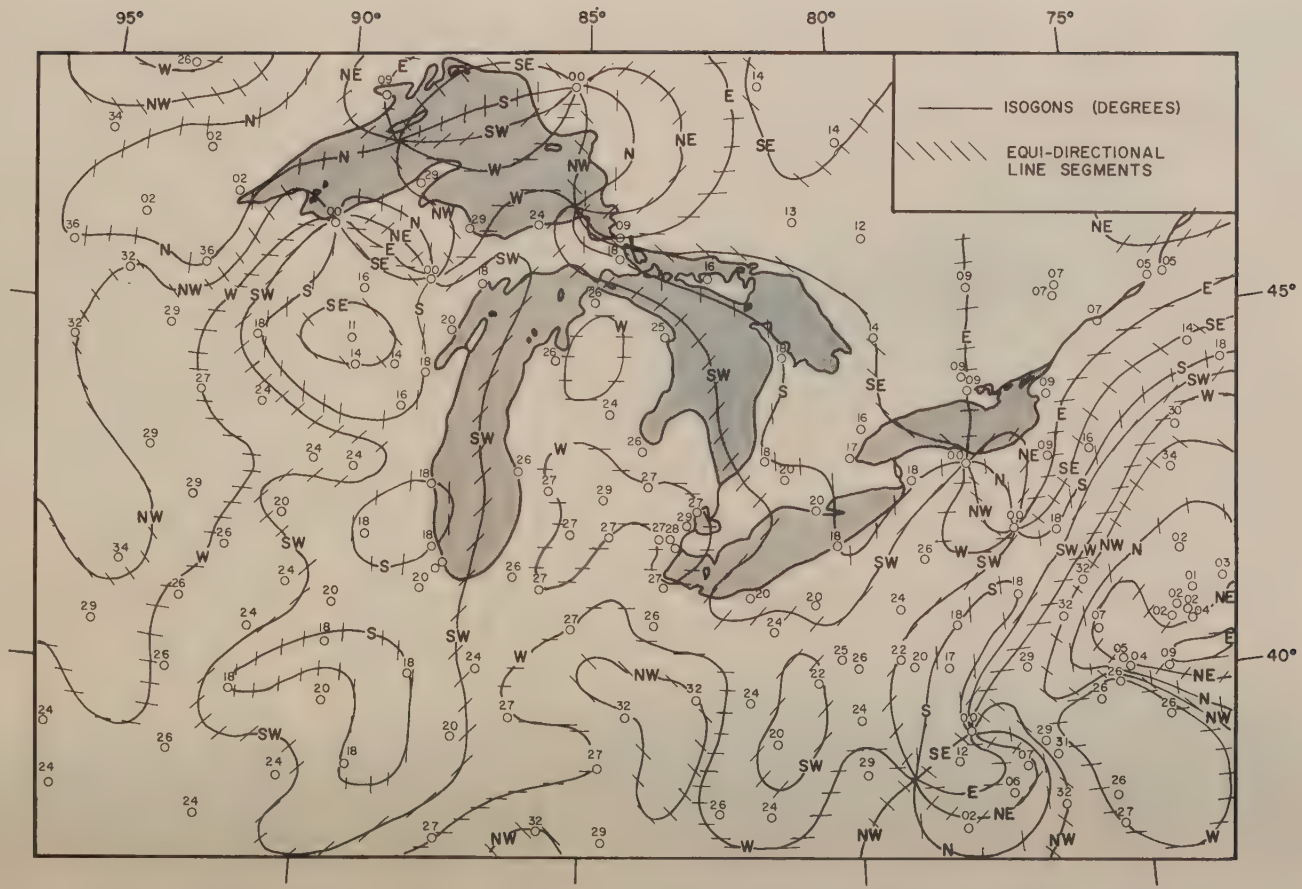

Fig. 11. Isogon analysis. Data above station circle wind direction in tens of degrees. Solid lines isogons. Broken lines equi-directional line segments.

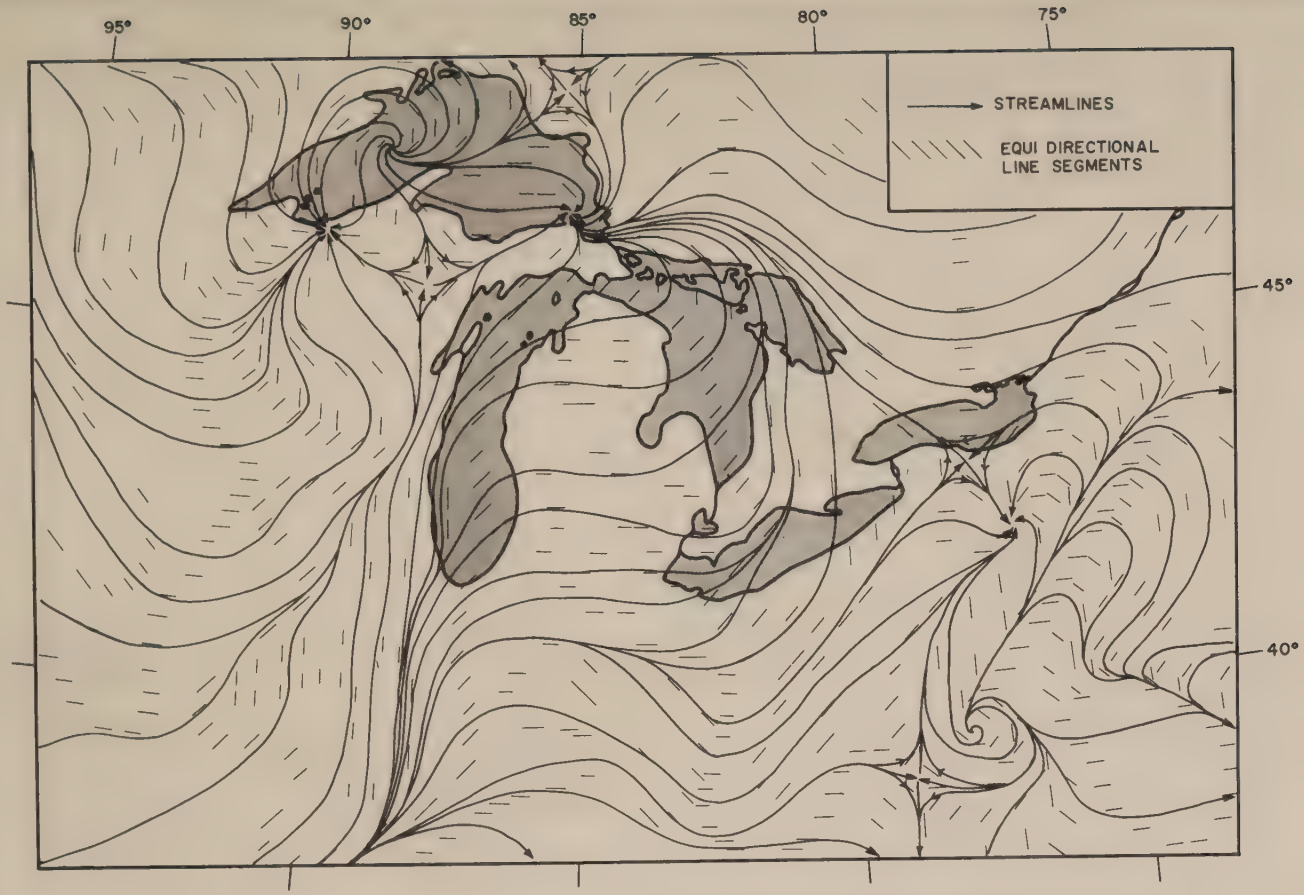

Fig. 12. Streamline analysis. Broken lines equi-directional line segments. Solid lines streamlines.

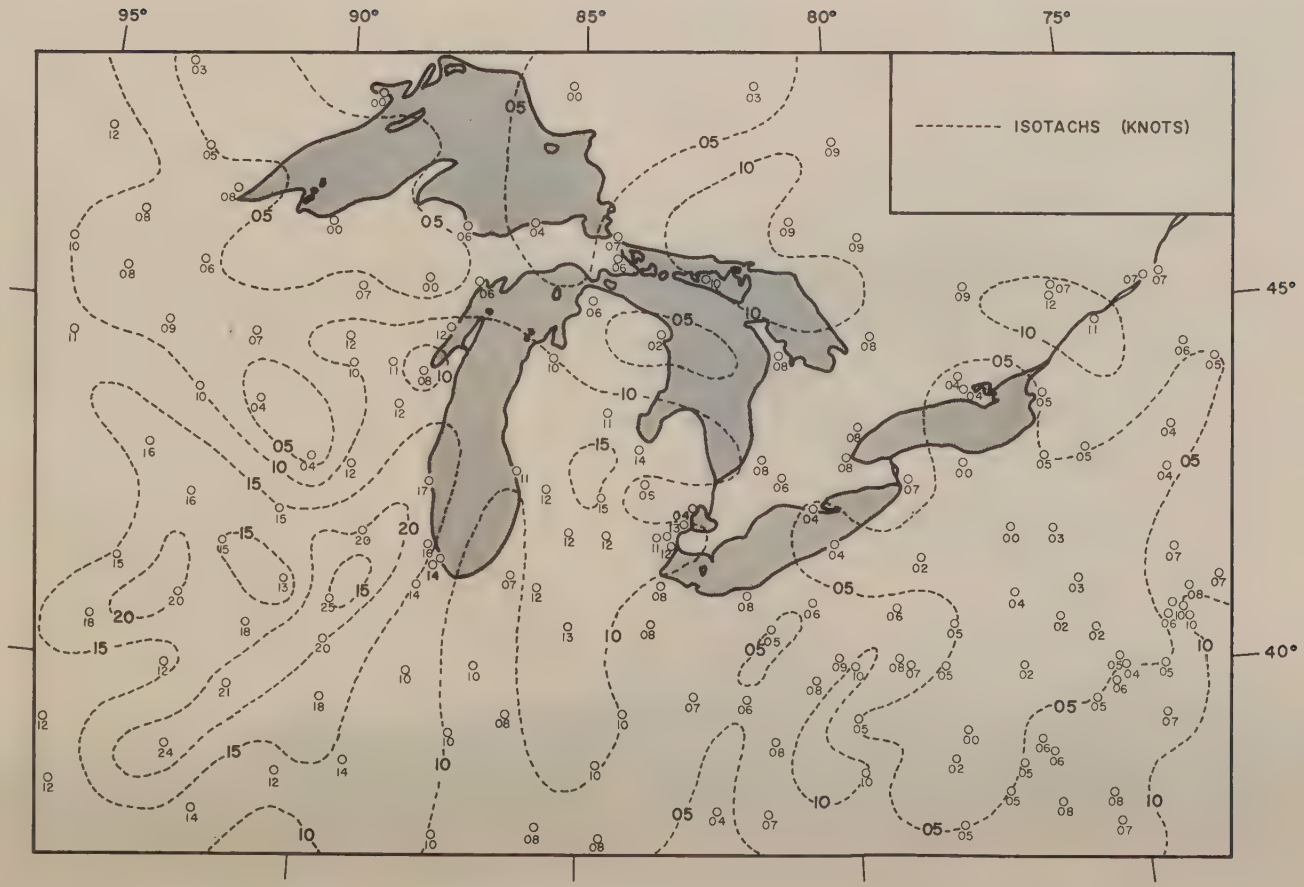

Fig. 13. Isotach analysis. Data beneath station circle wind speed in knots. Dashed lines isotachs.

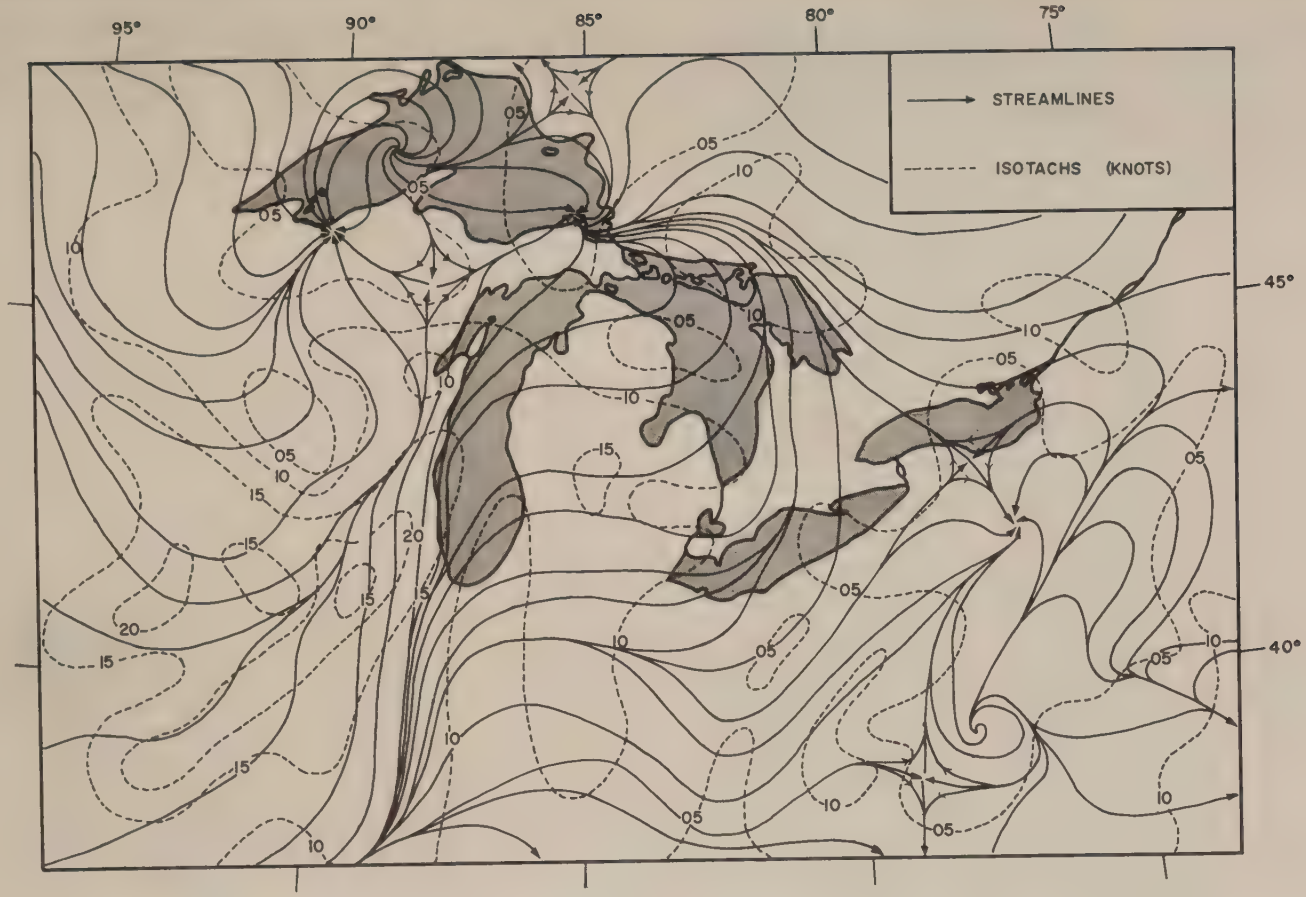

Fig. 14. Completed streamline-isotach analysis for 1300 EST, 23 October 1958. Solid lines streamlines; dashed lines isotachs.

is calm and the wind is considered omni-directional. The number of streamlines constructed is arbitrary.

Figure 12 is a completed analysis of the wind direction field over the Great Lakes and vicinity. The complete wind field, however, is not specified until its speed is analyzed. This is shown in Figure 13, where the two-digit figure appearing beneath the station circles is the wind speed in knots. The dashed lines are equal-speed isopleths (isotachs) drawn to the numerical data in intervals of 5 knots. The patterns in the figure show the variation in speeds of the air motion.

When isotachs are superimposed on streamlines, the resulting chart gives a complete representation of the horizontal wind field. This is shown in Figure 14. The speed and direction of the wind at any point over land or lake is given either directly when the streamlines or isotachs pass over the point, or by linear interpolation between isopleths when the desired location falls between them. The effect of the wind stress on surface water movement can be computed at this point by any suitable technique such as those described by Ayers *et al.* (1958) and Hunt (1958).

The streamline technique of representing the wind field at the water-air interface will give more definitive surface current patterns than from conventional techniques. This means increased knowledge of trajectories of water sampled for various physical and chemical parameters. The wind field portrayed will be no more accurate than is commensurate with the accuracy and density of individual data sources, but from a given set of data the technique provides the most accurate analysis of the wind velocity field. Historical as well as present wind data may be analyzed by the streamline technique.

ENVIRONMENTAL HISTORY OF LAKE ERIE

RAINFALL SINCE 1810

As a part of the accumulation of the historic background of the Lake Erie aquatic environment, searches of the literature for old meteorological data have been carried out. During these searches, there were uncovered sufficient rainfall data to allow the reconstruction of a practically continuous rainfall graph extending back to 1810. As is also the case with lake levels, it is greatly to be desired that rainfall records be extended back into the period when the Great Lakes watersheds were in essentially full-forest condition.

The oldest rainfall records pertaining to the Ohio region are from a gauge maintained by a Dr. Hildreth of Marietta, Ohio, during the years 1819-1823 and 1828-1832. These records, however, overlap with records from a gauge at the Pennsylvania Hospital in Philadelphia during the years 1810-1819, and 1827-1837. The overlap of the Marietta and Philadelphia records covered the 5-year period 1828-1832. The data for the overlap period are in terms of total rainfall and mean annual rainfall during the periods. Figures for the individual years are not available. The mean annual rainfall at Marietta was slightly greater than that at Philadelphia, and all the data from Philadelphia have been increased by an amount sufficient to make Philadelphia equal to Marietta during the period of overlap. The corrected Philadelphia data undoubtedly are in error, but to date they are all that are available for the 1810-1827 period. They have been used, as corrected, in the computation of the mean annual rainfall of the 1810-1958 period (discussed below). No attempt has been made to correct the Marietta records to stations within the Lake Erie basin. As the data now stand, they show a good degree of agreement with the old lake levels (discussed later): high lake levels following at the end of periods of above-average rainfall and low lake levels coming at the ends of periods of below-average rainfall.

Rainfall records, pertaining to the Lake Erie region directly, for the period 1838 through 1850 are from a gauge at Western Reserve University at Hudson, Ohio.

Rainfall data for the year 1859 are available, to date, only for Lake Huron. This has been converted to an estimate for Lake Erie by using the rainfall ratio of the two lakes for the ten-year period 1871-1880 inclusive. The Lake Huron figure for 1859 and figures for Lake Erie in 1860-1867 inclusive are from an early report of the Chief of Engineers, U. S. Army Engineers. The reference to this source and to the others used are indicated with the data in Table VIII and given in full in the Bibliography.

Precipitation data for the land area of Lakes Erie-St. Clair are given by Horton and Grunsky (1927). These data cover the years 1871 through 1922. Data of the U. S. Lake Survey, for the years 1900-1958, were very kindly provided by Mr. W. T. Laidly of the Survey. The overlap years (1900-1922) between Horton and Grunsky and the U. S. Lake Survey allow an assessment of the degree to which the inclusion of the Lake St. Clair basin by Horton and Grunsky may have interfered with the strict applicability of their data to the Lake Erie basin alone. Maximum variation between the two sets of data in the overlap years was 2.27 inches; minimum variation was 0.04 inches, with Horton and Grunsky being higher in both cases. The mean variation during the 23 years of overlap was 0.19 inch, with Horton and Grunsky being the lower. The overlap years and the comparison of Horton and Grunsky to the Lake Survey are shown in Table VIII.

Total rainfall in the years for which there are figures has been summed

Table VIII. Rainfall Since 1810

Philadelphia (Foster and Whitney, Pt. II, p. 337)

given: 1810-15* (5 years) 185.68 inches.
1815-19 (5 years) 151.14 inches.
1827-37 (11 years) 451.05 inches. Annual mean 41.00 inches.

*Taken as 1810-14, inclusive.

corrected: 1810-14, incl. 206.64 inches. Annual mean = 41.33 inches.
1815-19, incl. 168.20 inches. Annual mean = 33.64 inches.
1827-37, incl. 501.93 inches. Annual mean = 45.63 inches.

Marietta, Ohio (Foster and Whitney, Pt. II, p. 337)

1819-23 (5 years) 202.83 inches. Annual mean = 40.57 inches.
1828-32** (5 years) 228.17** inches. Annual mean = 45.63 inches.

**Omitted in computing mean of 1810-1958 period.

Hudson, Ohio (Foster and Whitney, Pt. II, p. 338)

mean of 1838, 1839, 1840 34.12 inches
1841 28.43 inches
1842 36.11 inches
1843 26.74 inches
1844 35.73 inches
mean of 1848, 1849, 1850 39.365 inches

Lake Huron (Rept. Chief of Engin. for 1868, Pt. II, p. 991)

given: 1859 27.90 inches

corrected: 1859 29.02 inches for Lake Erie

Lake Erie (Rept. Chief of Engin. for 1868, Pt. II, p. 991)

1860 31.29 inches
1861 35.58 inches
1862 36.58 inches
1863 31.69 inches
1864 34.00 inches
1865 32.67 inches
1866 38.15 inches
1867 28.61 inches

Table VIII (Continued)

Lake Erie—St. Clair (Horton and Grunsky, 1927, Table 46, p. 112)

1871	30.9 inches
1872	29.9 inches
1873	38.8 inches
1874	29.2 inches
1875	33.6 inches
1876	39.5 inches
1877	35.3 inches
1878	45.3 inches
1879	35.3 inches
1880	40.5 inches
1881	41.2 inches
1882	37.1 inches
1883	38.4 inches
1884	32.3 inches
1885	37.4 inches
1886	32.9 inches
1887	31.6 inches
1888	29.9 inches
1889	29.5 inches
1890	41.9 inches
1891	32.3 inches
1892	38.4 inches
1893	36.0 inches
1894	30.5 inches
1895	28.5 inches
1896	34.7 inches
1897	31.9 inches
1898	35.3 inches
1899	29.2 inches
1900	32.6 inches
1901	30.5 inches
1902	36.7 inches
1903	36.4 inches
1904	32.6 inches
1905	31.9 inches
1906	32.6 inches
1907	34.7 inches
1908	30.3 inches
1909	36.7 inches
1910	33.6 inches
1911	36.0 inches
1912	34.3 inches
1913	38.1 inches
1914	33.6 inches
1915	34.7 inches
1916	34.0 inches
1917	37.4 inches
1918	31.9 inches
1919	32.3 inches
1920	33.6 inches
1921	34.3 inches
1922	30.9 inches

U. S. Lake Survey—Lake Erie

32.53 inches	diff.	0.07	average	32.57
30.46 inches		0.04	(used in	30.48
36.49 inches		0.21	computing	36.60
36.09 inches		0.31	mean of	36.25
34.16 inches		-1.56	1810-1958)	33.38
33.58 inches		-1.68		32.74
33.62 inches		-1.02		33.11
36.21 inches		-1.51		35.46
30.91 inches		-0.61		30.61
38.00 inches		-1.30		37.35
33.38 inches		0.22		33.49
35.52 inches		0.48		35.76
34.66 inches		0.36		34.48
38.05 inches		0.05		38.08
33.23 inches		0.37		33.42
35.61 inches		-0.91		35.16
33.83 inches		0.17		33.92
35.13 inches		2.27		36.27
31.39 inches		0.51		31.65
32.67 inches		-0.37		32.49
31.94 inches		1.66		32.77
35.07 inches		-0.77		34.69
31.69 inches		-0.72		31.26
	Total	-4.45		
	Mean diff.	-0.19		

U. S. Lake Survey

1923	32.26 inches
1924	32.98 inches
1925	30.62 inches
1926	39.01 inches
1927	35.47 inches
1928	31.20 inches
1929	38.81 inches
1930	26.77 inches
1931	31.59 inches
1932	34.58 inches
1933	28.53 inches
1934	24.88 inches
1935	29.96 inches
1936	28.70 inches
1937	40.24 inches
1938	33.56 inches
1939	31.19 inches
1940	36.44 inches
1941	26.53 inches
1942	38.58 inches
1943	35.57 inches
1944	30.18 inches
1945	40.25 inches
1946	30.07 inches
1947	38.91 inches
1948	36.26 inches
1949	34.54 inches
1950	42.63 inches
1951	37.41 inches
1952	31.00 inches
1953	28.85 inches
1954	38.13 inches
1955	33.29 inches
1956	36.25 inches
1957	38.24 inches
1958	31.12 inches

Table IX. Monthly Mean Lake Levels, Lake Erie, Above Mean Tide at New York, Feet. Cleveland Gauge Back Through 1855.
Underlining indicates change of one digit.

Month	1859	1858	1857	1856	1855	1854	1853	1852	1851	1850	1849	1848	1847	1846	1845	1844	1843	1842
Jan	574.08	573.85	571.74	573.25	572.39				571.03					571.06				572.76
Feb	573.86	573.45	571.77	572.85	572.08				571.51					570.72				
Mar	574.27	573.48		572.52	572.14				572.12		572.03			570.64				
Apr	574.84	573.59		573.01	572.43				572.15					571.01				572.61
May	574.72	573.85	573.50	572.97	572.95				572.56		572.78	572.23	572.57	571.98	573.07	572.98	572.73	573.27
June	574.69	575.21	573.88	573.35	573.23				573.09	572.11				572.27				
July	574.75	575.16	573.97	573.38	573.73				573.16	572.73				572.22				
Aug	574.45	575.07	573.93	573.23	573.95	573.17			573.17					572.05	572.48			
Sept	573.85	574.51	573.68	572.98	573.30	572.84			572.86						572.16			
Oct	574.06	574.41	573.22	572.32	573.54	572.70			572.63			572,71	572.27,		571.93			
Nov	573.88	573.99	573.76	572.20	573.61	573.00				571.39					571.64			
Dec	573.68	574.09	573.76	572.49	573.89	572.42				571.49					571.31			

Month	1841	1840	1839	1838	1837	1836	1835	1834	1833	1832	1831	1830	1829	1828	1827	1826	1825	1824
Jan	572.39	570.37	571.51		572.02													
Feb	572.39																	
Mar	572.36											569.86						
Apr	572.75	571.79																
May	573.27	571.86	573.27	574.36														
June	573.01	571.94	573.60	575.03	572.53	572.47	572.34	572.59	571.94	572.28		571.86	571.86	571.86		572.28	571.11	
July	572.57	572.15	573.85	575.11														
Aug	572.07		573.90	574.55	573.22	572.72						571.72		571.72				
Sept	571.52	571.60	573.10	574.14	571.61		571.84											
Oct	570.64	571.49	574.07	573.75														
Nov	570.56	571.30	572.29	572.29														
Dec	571.68	571.07		573.19														

Table IX (Continued)

Month	1823	1822	1821	1820	1819	1818	1817	1816	1815	1814	1813	1812	1811	1810	1809	1808	1807	1806
Jan																		lake low
Feb				568.44						568.25								
Mar													566.50					
Apr																		
May								571.86	570.11	570.75	568.25	567.25	566.33	566.00	566.00			
June		570.11		569.02	569.78				571.86									
July					569.36				573.11									
Aug				570.07														
Sept																		
Oct																		
Nov																		
Dec							570.36											

Month	1800-1802	1798	1796	1702
Jan		lake rising	Lake very low, possibly lowest of all; beach never been so broad and continuous since. Settlers entering Ohio drove teams on beach most of way from Buffalo to Cleveland.	Detroit settled by French
Feb				
Mar				
Apr				
May				
June	571.11			
July				
Aug				
Sept				
Oct				
Nov				
Dec				

and divided by the number of years for which there are figures. These figures, including the corrections, indicated above, yield a mean annual rainfall value of 35.55 inches for the period 1810-1958.

Years of above-average and below-average rainfall are as follows. All hyphenated figures are inclusive.

Above Average	Below Average	Above Average	Below Average
1810-1814	1815-1819	1909	1912
1819-1837	1838-1841	1913	1914-1916
1842	1843	1917	1918-1925
1848-1850	1860	1926	1928
1862	1863-1865	1929	1930-1936
1866	1867	1937	1938-1939
1873	1871-1872	1940	1941
1876	1874-1875	1942	1944
1878	1884	1945	1946
1880-1883	1886-1889	1947-1948	1949
1885	1891	1950-1951	1952-1953
1890	1894-1901	1954	1955
1892-1893	1904-1908	1956-1957	1958
1902-1903	1910		

Years not specifically listed fell practically on the average.

PRE-1860 LAKE LEVELS

In the search for indices of past conditions of the aquatic environment of Lake Erie, we have come across a fairly substantial amount of data on lake levels of the years prior to 1860. While these old lake level records are at present of chiefly academic interest, they do have at least potential value in the search for indices inasmuch as they express the integrated effects of hydrology and progressive deforestation. The present hydrograph of lake levels put out by the U. S. Lake Survey, in extending back only through 1860, does not reach to the period when the Great Lakes watersheds were in essentially full-forest conditions. The present study allows the delineation of periods of high and low lake levels back to 1796. Accuracy of the lake height figures falls off as one goes into the period earlier than the high-water of 1838, but appears to be substantial back to the low-water of 1819-20. Earlier than the latter period, the records become predominantly the recollections of early settlers and are decreasingly accurate, but at least approximate figures can be deduced back to 1800-02. Prior to that time the data are merely qualitative.

High-waters are indicated in 1858-59, 1838, 1815-16, and 1800-02. Low-waters are indicated for the years 1819-20, 1809-10, and 1796. Also indicated quite clearly is a progressive downward trend in lake level from 1860-1796. The meaning of the latter is unknown, but it might be a reflection of the presence of the forest with its concomitant increased water loss in transpiration, interception, and retention.

The complete lake level data are given in Table IX; they have been obtained from the following sources (see Bibliography for complete references): Houghton *et al.* (1839); U. S. Army Engineers (1870); Foster and Whitney (1851); Gilbert (1898); Houghton *et al.* (1839); Houghton *et al.* (1840); U. S. Army Engineers (1904).

LAKE ERIE WATER CHEMISTRY SINCE 1854

As a part of the program of assembling background information on the condition of the Lake Erie aquatic environment, search was made for chemical analyses of Lake Erie water. Suitable data of this type are not abundant, but enough were found to allow reconstruction of certain trend lines of chemical composition for the period 1854 to 1956. The data, together with indications of the source papers, are given in Table X. None of these analyses appear to be suspect, except for silica in the two sets of earlier determinations. Older silica values in these and other analyses are materially higher than are obtained by modern methods.

Three areas of Lake Erie were found in which direct comparisons of old and recent data were possible. These are the Detroit River (1854 and 1948-49); Erie, Pennsylvania (1901-03 and 1956); and the east end of the lake (Buffalo, 1906-07 and Fort Erie and Chippewa, 1948-49). The few data available from Fort Erie have been averaged here with those of Chippewa.

	Detroit River		Erie, Pa.		East End	
	Detroit 1854	Windsor 1948-49	1901-03	1956	Buffalo 1906-07	Ft. Erie-Chippewa 1948-49
Alkalinity			98.8	90.0	98	
Silica	5.0	3.8		1.5	5.9	1.9
Iron	3.9	0.75		0.1	0.07	0.04
Calcium	20.0	28.0		36.0	31.0	38.5
Magnesium		8.0		8.9	7.6	8.7
Sodium plus potassium	3.7	4.8		8.7	6.5	9.8
Carbonate		1.4			3.1	0.9
Bicarbonate		103.		152.	114.	108.
Sulphate	6.6	17.4		23.0	13.0	22.7
Nitrate		1.4	0.09	0.40	0.3	0.25
Chloride		6.5	6.4	20.0	8.7	18.2
Total solids	98.1	131.0	144.0	171.0	133.0	168.0

In the Detroit River, increases are particularly notable in calcium, sodium plus potassium, sulphate, and total solids, while a decrease occurred in iron. At Erie only four analyses are available from 1901-03; these show definite increases in nitrate, chloride, and total solids, and a decrease in total alkalinity. In the east end increases occurred in calcium, magnesium, sodium plus potassium, sulphate, chloride, and total solids; decreases are evident in silica, iron, carbonate, bicarbonate, and nitrate. Some of these changes are small, while some, particularly the sulphate, chloride, and total solids, show relatively great increases in concentration.

From Lorain 1950-52 was obtained the ratio of alkalinity to each of the other chemical constituents. These ratios were applied to the monthly alkalinity values obtained at the Lorain water plant to obtain approximate chemical compositions of the western basin water during the 1948-56 period of record of this plant. These monthly chemical estimates and annual means derived from them are given in Appendix I.

Table X. Chemical Analyses, Lake Erie Water, PPM

	Detroit River			Ashtabula	Off Erie	Buffalo	Off Ashtabula
	1854[a]	1882[a]	1897[a]	1901[b]	1901-03[c]	1906-07[d]	31 Jan. 1925[e]
Alkalinity					98.8	98.*	105.
Silica	5.0	7.2				5.9	
Iron	3.9					0.07	
Calcium	20.	26.4	23.			31.	
Magnesium		7.4				7.6	
Sodium plus potassium	3.7					6.5	
Carbonate						3.1	
Bicarbonate				110.		114.	
Sulphate	6.6	4.6				13.	
Nitrate				0.1	0.09	0.3	0.06
Chloride		7.5		5.1	6.4	8.7	15.
Total solids	98.1	117.1	108.	159.	144.	133.	160.

	Off Conneaut	Off Fairport	Cleveland				Windsor
	31 Jan. 1925[e]	4 Feb. 1925[e]	1928[f]	1929[f]	1930[f]	1937[f]	1934-38[f]
Alkalinity	75 (?)	105.					77.8
Silica							2.8
Iron			0.61	0.64	0.79	0.37	0.12
Calcium							30.7
Magnesium					9.3	9.5	8.6
Sodium plus potassium							
Carbonate							
Bicarbonate							94.9
Sulphate							16.0
Nitrate	0.21	0.04					0.3
Chloride	7.	42.					4.5
Total solids	140.	235.					148.0

	Port Colborne	Fort Erie	Cleveland					
	1934-37[f]	1934-38[f]	1938[g]	1939[g]	1940[g]	1941[g]	1942[g]	1943[g]
Alkalinity	94.0	93.2						
Silica		4.2						
Iron	0.05	0.07	0.44	0.42	0.34	0.29	0.42	
Calcium	37.6	36.1						
Magnesium	9.4	9.2	9.2	9.1	8.6	8.7	8.8	8.7
Sodium plus potassium								
Carbonate								
Bicarbonate	114.6	113.7						
Sulphate		23.2						
Nitrate		1.6						
Chloride		16.5						
Total solids		165.0						

*Calculated or back-calculated (**) by method of Palmer (1911).

[a]From U.S. Geol. Surv. Water-Supply Paper No. 31. Analyses of 1854 and 1882 have been reduced from hypothetical combinations.

[b]Ashtabula, low pressure data, pp. 164-5 *in* Foulk (1925).

[c]From U.S. Geol. Surv. Water-Supply and Irrigation Paper No. 161.

[d]From U.S. Geol. Surv. Water-Supply Paper 236, also in U.S. Geol. Surv., Prof. Paper 135.

[e]Personal communication, U.S. Engineer Office, Buffalo, N.Y., to U.S. Fish and Wildlife Service, Ann Arbor. Ammonia fractions, nitrite, BOD also given. Single samples only.

[f]From Leverin, 1947, pp. 89-90, 97, 102.

[g]Data of the Division and Baldwin water plants at Cleveland, collected by the present contract. Yearly averages derived from monthly averages at the plants.

Table X (Continued). Chemical Analyses, Lake Erie Water, PPM

	Cleveland				Windsor	Ft. Erie-Chippewa
	1944[g]	1946[g]	1947[g]	1948[g]	1948-49[h]	1948-49[h]
Alkalinity						
Silica					3.8	1.9
Iron					0.75	0.04
Calcium					28.0	38.5
Magnesium	9.1	8.9	8.5	8.6	8.0	8.7
Sodium plus potassium					4.8	9.8
Carbonate					1.4	0.9
Bicarbonate					103.0	108.0
Sulphate					17.4	22.7
Nitrate					1.4	0.25
Chloride					6.5	18.2
Total solids					131.0	168.0

	Port Stanley, Ont.	Lorain	Erie
	1948-49[h]	1950-52[i]	1956[j]
Alkalinity		91.*	90.
Silica	1.3	1.9	1.5
Iron	0.02	0.04	0.1
Calcium	38.	36.	36.
Magnesium	7.7	8.5	8.9
Sodium plus potassium	9.2	9.5	8.7
Carbonate	0.4	8.0	
Bicarbonate	107.	113.	152.**
Sulphate	42.4	25.	23.
Nitrate	1.14	1.2	0.4
Chloride	17.8	18.	20.
Total solids	174.	165.	171.

*Calculated or back-calculated (**) by method of Palmer (1911).
[h]From Thomas, 1954, pp. 24-31.
[i]Average of numerous samples throughout the year at the Lorain water plant, from Lake Erie Pollution Survey Supplement, 1953.
[j]From Ninetieth Annual Report of the City of Erie.

THE METROPOLITAN POPULATION INDEX

It is almost axiomatic that the quantities of foreign material entering a body of water are in proportion to the level of human population around that water body. The materials that enter Lake Erie as direct and indirect effects of man's presence can be represented in a rough and qualitative way by the human population in the metropolitan belt that surrounds the west and south sides of the lake.

To this end the sum of populations of Detroit, Toledo, Cleveland, Erie, and Buffalo have been taken as an index of the probable magnitude of man's total effects on Lake Erie. As a convenient reference the population of metropolitan Chicago is also included.

Census	Erie Index	Chicago
1950	3,778,927	3,620,962
1940	3,476,993	3,396,808
1930	3,448,952	3,376,438
1920	2,633,830	2,701,705
1910	1,685,166	2,185,283
1900	1,204,414	1,698,575
1890	844,961	1,099,850
1880	509,494	503,185
1870	337,350	298,977
1860	193,352	112,172
1850	90,001	29,963
1840	38,020	4,470
1830	13,431	---
1820	4,758	---

From these figures it is apparent that Lake Erie between 1820 and 1890 had a heavier population-pressure than the city of Chicago could have provided. From 1890 through 1920 Chicago contained somewhat more people than the metropolitan belt of Lake Erie, but since 1930 Lake Erie has had a metropolitan population larger than that of Chicago. Sewage and industrial wastes from the Lake Erie metropolitan areas enter the lake. When it is remembered that Lake Erie contains only about 99 cubic miles of water, it becomes reasonable to expect that the lake may be reflecting in its chemistry the effects of human population-pressure. Except for the plant-nutrient chemicals (silica, nitrate, and possibly iron) and alkalinity, the chemical constituents of the lake have increased very significantly in the past century.

CONCLUSION

The results and techniques presented in this report have come from the Lake Erie pilot study on the usefulness of the data being accumulated by municipal and industrial users of lake water. They show that these data have a potential in understanding past events in the lake and in "watching" the lake for the development of trends in the future.

The pilot study and the studies of past aquatic conditions that have accompanied it have made available a substantial amount of new information and techniques which may help explain the causes of past fluctuations in the commercial fisheries and contribute to our understanding of the more academic problem of eutrophication of lakes.

There are still a number of facets of the past conditions of the aquatic environment that have yet to be studied. Among these may be mentioned the assembly of a record of past unusually severe or unusually mild meteorological conditions and their probable effects on the lake, further search for biological indications of changing or changed conditions in the water, and the development of a set of criteria by which the data from representative water-user installations can be watched for the development of trends favorable or unfavorable for commercially important fish species.

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APPENDIX I

CHEMICAL VALUES BASED ON TOTAL ALKALINITY AT LORAIN, OHIO

Year 1948

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.	Ratio**
Temp. (Avon)	1.7	1.4	4.4	9.9	14.8	19.9	23.7	23.8	21.9	13.8	9.7	5.8	12.6	
Temp. (Lorain)														
Total solids	163	161	157	154	156	163	163	161	159	159	165	161	160	1.81
Nitrate	1.19	1.17	1.15	1.12	1.14	1.19	1.19	1.17	1.16	1.16	1.20	1.17	1.17	.0132
Fluoride	.10	.10	.10	.09	.09	.10	.10	.10	.10	.10	.10	.10	.10	.0011
Chloride	17.8	17.6	17.2	16.8	17.0	17.8	17.8	17.6	17.4	17.4	18.0	17.6	17.5	.198
Sulphate	24.7	24.5	23.9	23.4	23.7	24.7	24.7	24.5	24.2	24.2	25.0	24.5	24.3	.275
Bicarbonate	112	110	108	105	107	112	112	110	109	109	113	110	110	1.24
Sodium plus potassium	9.4	9.3	9.0	8.8	8.9	9.4	9.4	9.3	9.2	9.2	9.5	9.3	9.2	.104
Magnesium	8.4	8.3	8.1	7.9	8.0	8.4	8.4	8.3	8.2	8.2	8.5	8.3	8.2	.093
	10*	6.4*	5.9*	5.5*	6.2*	6.6*	6.2*	6.7*	6.4*	6.4*	6.5*	6.3*		
Calcium	35.5	35.2	34.4	33.6	34.0	35.5	35.5	35.2	34.8	34.8	35.9	35.2	35.0	.395
Iron	.04	.04	.03	.03	.03	.04	.04	.04	.04	.04	.04	.04	.04	.0004
Silica	1.9	1.9	1.8	1.8	1.8	1.9	1.9	1.9	1.8	1.8	1.9	1.9	1.9	.021
Alkalinity	90	89	87	85	86	90	90	89	88	88	91	89	88.5	1.0

*Observed magnesium

**The "ratio" values indicated are the ratio of the parameter in question to alkalinity, i.e., "ratio" = parameter/alkalinity. These values apply to years 1948-1956, pages 54 to 62.

Year 1949

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	4.1	3.9	5.2	9.5	15.6	21.4	25.2	25.4	19.7	16.6	8.7	4.3	13.3
Temp.(Lorain)													
Total solids	159	159	159	154	156	156	159	163	161	163	165	157	159
Nitrate	1.16	1.16	1.16	1.12	1.14	1.14	1.16	1.19	1.17	1.19	1.20	1.15	1.16
Fluoride	.10	.10	.10	.09	.09	.09	.10	.10	.10	.10	.10	.10	.10
Chloride	17.4	17.4	17.4	16.8	17.0	17.0	17.4	17.8	17.6	17.8	18.0	17.2	17.4
Sulphate	24.2	24.2	24.2	23.4	23.7	23.7	24.2	24.7	24.5	24.7	25.0	23.9	24.2
Bicarbonate	109	109	109	105	107	107	109	112	110	112	113	108	109
Sodium plus potassium	9.2	9.2	9.2	8.8	8.9	8.9	9.2	9.4	9.3	9.4	9.5	9.0	9.2
Magnesium	8.2	8.2	8.2	7.9	8.0	8.0	8.2	8.4	8.3	8.4	8.5	8.1	8.2
	6.5*	6.4*	7.4*	6.7*	5.9*	5.7*	5.7*	5.5*	5.4*	5.5*	5.2*	5.1*	
Calcium	34.8	34.8	34.8	33.6	34.0	34.0	34.8	35.5	35.2	35.5	35.9	34.4	34.8
Iron	.04	.04	.04	.03	.03	.03	.04	.04	.04	.04	.04	.03	.04
Silica	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.9	1.9	1.9	1.9	1.8	1.8
Alkalinity	88	88	88	85	86	86	88	90	89	90	91	87	88

*Observed magnesium

Year 1950

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	4.8	3.2	2.2	6.8	11.9	19.4	21.9	23.4	20.3	16.0	9.2	2.7	11.8
Temp.(Lorain)													
Total solids	145	147	148	154	154	163	165	165	167	165	163	154	157
Nitrate	1.06	1.07	1.08	1.12	1.12	1.19	1.20	1.20	1.21	1.20	1.19	1.12	1.15
Fluoride	.09	.09	.09	.09	.09	.10	.10	.10	.10	.10	.10	.09	.10
Chloride	15.8	16.0	16.2	16.8	16.5	17.8	18.0	18.0	18.2	18.0	17.8	16.8	17.2
Sulphate	22.0	22.3	22.5	23.4	23.4	24.7	25.0	25.0	25.3	25.0	24.7	23.4	23.9
Bicarbonate	99	100	102	105	105	112	113	113	114	113	112	105	108
Sodium plus potassium	8.3	8.4	8.5	8.8	8.8	9.4	9.5	9.5	9.6	9.5	9.4	8.8	9.0
Magnesium	7.4 6.2*	7.5 5.7*	7.6 6.3*	7.9 7.6*	7.9 8.3*	8.4 9.2*	8.5 9.1*	8.5 8.9*	8.6 8.5*	8.5 8.5*	8.4 8.5*	7.9 8.8*	8.1
Calcium	31.6	32.0	32.4	33.6	33.6	35.5	35.9	35.9	36.3	35.9	35.5	33.6	34.3
Iron	.03	.03	.03	.03	.03	.04	.04	.04	.04	.04	.04	.03	.03
Silica	1.7	1.7	1.7	1.8	1.8	1.9	1.9	1.9	1.9	1.9	1.9	1.8	1.8
Alkalinity	80	81	82	85	85	90	91	91	92	91	90	85	86.9

*Observed magnesium

Year 1951

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	2.2	2.0	5.4	8.0	13.8	20.5	23.3	23.9	20.7	16.0	7.4	3.6	12.2
Temp.(Lorain)													
Total solids	157	157	163	161	167	176	176	181	181	181	172	165	170
Nitrate	1.15	1.15	1.19	1.17	1.21	1.28	1.28	1.32	1.32	1.32	1.25	1.20	1.24
Fluoride	.10	.10	.10	.10	.10	.11	.11	.11	.11	.11	.10	.10	.10
Chloride	17.2	17.2	17.8	17.6	18.2	19.2	19.2	19.8	19.8	19.8	18.8	18.0	18.6
Sulphate	23.9	23.9	24.7	24.5	25.3	26.7	26.7	27.5	27.5	27.5	26.1	25.0	25.8
Bicarbonate	108	108	112	110	114	120	120	124	124	124	118	113	116
Sodium plus potassium	9.0	9.0	9.4	9.3	9.6	10.1	10.1	10.4	10.4	10.4	9.9	9.5	9.7
Magnesium	8.1 8.6*	8.1 8.6*	8.4 9.1*	8.3 9.0*	8.6 9.3*	9.0 9.3*	9.0 8.8*	9.3 8.7*	9.3 8.8*	9.3 8.7*	8.8 8.6*	8.5 8.3*	8.7
Calcium	34.4	34.4	35.5	35.2	36.3	38.3	38.3	39.5	39.5	39.5	37.5	35.9	37.0
Iron	.03	.03	.04	.04	.04	.04	.04	.04	.04	.04	.04	.04	.04
Silica	1.8	1.8	1.9	1.9	1.9	2.0	2.0	2.1	2.1	2.1	2.0	1.9	2.0
Alkalinity	87	87	90	89	92	97	97	100	100	100	95	91	93.7

*Observed magnesium

Year 1952

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	3.2	2.4	2.8	8.0	13.1	20.8	24.5	24.1	21.7	14.8	8.7	5.1	12.4
Temp.(Lorain)													
Total solids	161	157	150	154	161	168	167	172	172	174	176	168	165
Nitrate	1.17	1.15	1.10	1.12	1.17	1.23	1.21	1.25	1.25	1.27	1.28	1.23	1.20
Fluoride	.10	.10	.09	.10	.10	.10	.10	.10	.10	.11	.11	.10	.10
Chloride	17.6	17.2	16.4	16.8	17.6	18.4	18.2	18.8	18.8	19.0	19.2	18.4	18.1
Sulphate	24.5	23.9	22.8	23.4	24.5	25.6	25.3	26.1	26.1	26.4	26.7	25.6	25.1
Bicarbonate	110	108	103	105	110	115	114	118	118	119	120	115	113
Sodium plus potassium	9.3	9.0	8.6	8.8	9.3	9.7	9.6	9.9	9.9	10.0	10.1	9.7	9.5
Magnesium	8.3	8.1	7.7	7.9	8.3	8.6	8.6	8.8	8.8	8.9	9.0	8.6	8.5
	8.3*	8.5*	8.2*	8.3*	9.9*	8.1*	8.2*	8.3*	8.4*	8.1*	8.5*	8.3*	
Calcium	35.2	34.4	32.8	33.6	35.2	36.7	36.3	37.5	37.5	37.9	38.3	36.7	36.0
Iron	.04	.03	.03	.03	.04	.04	.04	.04	.04	.04	.04	.04	.04
Silica	1.9	1.8	1.7	1.8	1.9	2.0	1.9	2.0	2.0	2.0	2.0	2.0	1.9
Alkalinity	89	87	83	85	89	93	92	95	95	96	97	93	91.2

*Observed magnesium

Year 1953

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	3.6	3.6	4.6	8.2	12.6	19.1	23.5	24.5	21.8	16.7	10.4	4.6	12.8
Temp.(Lorain)													
Total solids	163	157	157	159	157	161	163	165	167	167	161	165	162
Nitrate	1.19	1.15	1.15	1.16	1.15	1.17	1.19	1.20	1.21	1.21	1.17	1.20	1.18
Fluoride	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10
Chloride	17.8	17.2	17.2	17.4	17.2	17.6	17.8	18.0	18.2	18.2	17.6	18.0	17.7
Sulphate	24.7	23.9	23.9	24.2	23.9	24.5	24.7	25.0	25.3	25.3	24.5	25.0	24.6
Bicarbonate	112	108	108	109	108	110	112	113	114	114	110	113	111
Sodium plus potassium	9.4	9.0	9.0	9.2	9.0	9.3	9.4	9.5	9.6	9.6	9.3	9.5	9.3
Magnesium	8.4 8.8*	8.1 9.1*	8.1 8.8*	8.2 9.8*	8.1 9.1*	8.3 8.8*	8.4 8.8*	8.5 9.5*	8.6 8.5*	8.6 8.5*	8.3 8.4*	8.5 8.5*	8.3
Calcium	35.5	34.4	34.4	34.8	34.4	35.2	35.5	35.9	36.3	36.3	35.2	35.9	35.3
Iron	.04	.03	.03	.04	.03	.04	.04	.04	.04	.04	.04	.04	.04
Silica	1.9	1.8	1.8	1.8	1.8	1.9	1.9	1.9	1.9	1.9	1.9	1.9	1.9
Alkalinity	90	87	87	88	87	89	90	91	92	92	89	91	89.4

*Observed magnesium

Year 1954

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	1.6	2.8	3.5	9.0	13.2	19.7	23.7	23.6	21.3	16.6	9.1	3.8	12.3
Temp.(Lorain)													
Total solids	165	159	154	148	161	161	157	165	167	165	163	161	161
Nitrate	1.20	1.16	1.12	1.08	1.17	1.17	1.15	1.20	1.21	1.20	1.19	1.17	1.17
Fluoride	.10	.10	.09	.09	.10	.10	.10	.10	.10	.10	.10	.10	.10
Chloride	18.0	17.4	16.8	16.2	17.6	17.6	17.2	18.0	18.2	18.0	17.8	17.6	17.6
Sulphate	25.0	24.2	23.4	22.5	24.5	24.5	23.9	25.0	25.3	25.0	24.7	24.5	24.4
Bicarbonate	113	109	105	102	110	110	108	113	114	113	112	110	110
Sodium plus potassium	9.5	9.2	8.8	8.5	9.3	9.3	9.0	9.5	9.6	9.5	9.4	9.3	9.2
Magnesium	8.5	8.2	7.9	7.6	8.3	8.3	8.1	8.5	8.6	8.5	8.4	8.3	8.2
	8.1*	7.6*	7.7*	8.8*	8.9*	8.1*	8.3*	8.4*	8.6*	7.5*	8.2*	8.0*	
Calcium	35.9	34.8	33.6	32.4	35.2	35.2	34.4	35.9	36.3	35.9	35.5	35.2	35.0
Iron	.04	.04	.03	.03	.04	.04	.03	.04	.04	.04	.04	.04	.04
Silica	1.9	1.8	1.8	1.7	1.9	1.9	1.8	1.9	1.9	1.9	1.9	1.9	1.9
Alkalinity	91	88	85	82	89	89	87	91	92	91	90	89	88.7

*Observed magnesium

Year 1955

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	1.7	.9	3.8	8.9	15.7	19.4	24.9	25.7	21.7	16.2	8.1	1.9	12.4
Temp.(Lorain)													
Total solids	163	159	157	157	161	163	163	163	165	163			161
Nitrate	1.19	1.16	1.15	1.15	1.17	1.19	1.19	1.19	1.20	1.19			1.18
Fluoride	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10			.10
Chloride	17.8	17.4	17.2	17.2	17.6	17.8	17.8	17.8	18.0	17.8			17.7
Sulphate	24.7	24.2	23.9	23.9	24.5	24.7	24.7	24.7	25.0	24.7			24.5
Bicarbonate	112	109	109	109	110	112	112	112	113	112			111
Sodium plus potassium	9.4	9.2	9.0	9.0	9.3	9.4	9.4	9.4	9.5	9.4			9.3
Magnesium	8.4	8.2	8.1	8.1	8.3	8.4	8.4	8.4	8.5	8.4			8.3
			9.7*	7.2*	7.5*	8.0*	8.3*	8.7*	9.3*				
Calcium	35.5	34.8	34.4	34.4	35.2	35.5	35.5	35.5	35.9	35.5			35.2
Iron	.04	.04	.03	.03	.04	.04	.04	.04	.04	.04			.04
Silica	1.9	1.8	1.8	1.8	1.9	1.9	1.9	1.9	1.9	1.9			1.9
Alkalinity	90	88	87	87	89	90	90	90	91	90			89.2

*Observed magnesium

Year 1956

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yearly Av.
Temp.(Avon)	.8	.4	3.2	7.9	12.4	18.9	22.7	23.6		15.7	9.9	4.5	10.0
Temp.(Lorain)													
Total solids	163	154	157	163	161	161	161	165	168	170	167	168	163
Nitrate	1.19	1.12	1.15	1.19	1.17	1.17	1.17	1.20	1.23	1.24	1.21	1.23	1.19
Fluoride	.10	.09	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10	.10
Chloride	17.8	16.8	17.2	17.8	17.6	17.6	17.6	18.0	18.4	18.6	18.2	18.4	17.9
Sulphate	24.7	23.4	23.9	24.7	24.5	24.5	24.5	25.0	25.6	25.9	25.3	25.6	24.8
Bicarbonate	112	105	108	112	110	110	110	113	115	117	114	115	112
Sodium plus potassium	9.4	8.8	9.0	9.4	9.3	9.3	9.3	9.5	9.8	9.8	9.6	9.7	9.4
Magnesium	8.4	7.9 7.6*	8.1 9.2*	8.4 8.3*	8.3 7.7*	8.3 7.1*	8.3 8.4*	8.5 8.3*	8.6	8.7 9.2*	8.6	8.6	8.4
Calcium	35.5	33.6	34.4	35.5	35.2	35.2	35.2	35.9	36.7	37.1	36.3	36.7	35.6
Iron	.04	.03	.03	.04	.04	.04	.04	.04	.04	.04	.04	.04	.04
Silica	1.9	1.8	1.8	1.9	1.9	1.9	1.9	1.9	2.0	2.0	1.9	2.0	1.9
Alkalinity	90	85	87	90	89	89	89	91	93	94	92	93	90.2

*Observed magnesium

APPENDIX II

LIMNOLOGICAL OBSERVATIONS

Data of the Fisheries Research Laboratory of the University of Western Ontario.

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1947 and 1948
STATION I (42°12.0', 81°54.0')

Depth in Feet	1947								1948							
	8/8	8/13	8/21	8/28	9/14	9/27	10/17	12/3	4/15	4/23	5/6	7/8'	7/20	7/28	8/6	9/9
Water Temperature, °C																
Surface	23.8	25.0	26.8	25.9	23.7	16.4	18.3	6.0	3.0	4.7	10.0	19.3	23.5	20.7	18.3	22.0
15	23.2	24.2	25.7	25.6	23.7	16.3	17.3							19.7	18.1	
30	14.5	18.6	22.9	25.2	22.9	16.3	17.1	6.2				13.6	18.9	11.3	17.9	
Bottom	12.7	13.6	15.1	14.3	13.6	16.2	15.7	6.4	3.6	4.0	8.0		12.2	11.0	17.6	22.0
Dissolved Oxygen, ppm																
Surface	6.1	7.2	6.3	6.7	7.2	8.0	8.8		14.6	11.6	10.6		8.2	7.7	8.0	8.6
30	7.2	7.5				8.5	8.3							4.2	7.9	8.1
Bottom	7.1		6.1	6.0	6.7	6.3	7.7		14.6	11.5	11.6		4.2	4.1	5.6	7.3
Free Carbon Dioxide, ppm																
Surface									0.0	0.0	0.0		0.0	8.8	0.0	0.0
30					2.2								1.8	17.6	8.8	0.0
Bottom				3.5	1.5	2.6	0.8		0.0	0.0			1.3	17.6	17.6	0.0
Methyl Orange Alkalinity, ppm $CaCO_3$																
Surface			58	95	94	100	100	56	104	100	102		100	109	84	103
30					104	100	100						107	111	115	105
Bottom			58		110	96	100	57	104	100			112	115	114	124
Phenolphthalein Alkalinity, ppm $CaCO_3$																
Surface					3.0			1.6	4.0	4.0	5.0		0.0	0.0	8.0	6.0
30													0.0	0.0	0.0	3.0
Bottom									4.0	4.0			0.0	0.0	0.0	3.0
pH																
Surface	8.2	8.0	8.1	8.1	7.7	7.8	8.2		7.7	8.0	8.1		8.2	8.0	8.0	8.5
30		7.7	7.6		7.7	7.8	7.9						8.0	7.9	8.0	8.5
Bottom	7.4	7.6	7.8	7.3	7.4	7.8	7.8		7.8	8.1			7.6	8.0	8.0	8.5
Secchi Disc, feet																
	23	25			13											

1949, 1950, and 1951
STATION 1 (42°12.0', 81°54.0')

Depth in Feet	1949					1950					1951					
	6/19	7/12	7/20	8/4	8/23	5/29	6/7	8/26	9/1	11/5	5/30	6/28	7/13	7/18	8/2	8/28
Water Temperature, °C																
Surface	20.1	24.0	27.8	24.7	23.3	15.2	16.3	20.2	23.3	11.5	13.0	19.7	20.1	21.4	23.5	21.7
15	18.8	23.8	24.2	24.6	23.2	11.9	12.2						19.0	21.3		
30	17.1		23.8	23.9	22.9	10.0	8.1	20.0	21.9		11.3	17.0	18.7	17.5	23.3	21.3
Bottom	16.1	23.4	14.6	22.5	22.7	9.0	8.0	10.8	11.2	11.5	9.7	15.2	10.8	11.9	10.8	11.3
Dissolved Oxygen, ppm																
Surface	9.6	8.1	7.6		8.3	11.7	11.0	8.4		9.7	11.2	9.6		9.2		9.3
30	9.5	8.4	8.0		8.0	11.6	11.0	8.4			10.8	10.7		9.3		8.9
Bottom	8.0	7.9	6.4		7.9	10.9	10.8	7.6		9.6	10.8	9.3		8.3		4.5
Free Carbon Dioxide, ppm																
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.8	5.3		1.8		0.0
30	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0			3.5		2.6		0.0
Bottom	0.0	2.0	3.0	2.5	0.0	0.9	1.3	2.6	2.6	0.0	7.1	7.0		4.0		2.7
Methyl Orange Alkalinity, ppm $CaCO_3$																
Surface	108	90	116	114	116	111	98	106	103	105	108	107		108		105
30	104	110	114	110	116	122	110	106	104			109		108		102
Bottom	100	106	114	114	116	116	112	114	107	100	120	108		109		110
Phenolphthalein Alkalinity, ppm $CaCO_3$																
Surface	4.0	4.0	5.0	5.0	5.0	3.0	1.0	2.0	2.5	2.5	0.0	0.0	0.0	0.0		3.0
30	4.0	2.0	3.0	4.0	4.0	0.5	0.0	1.0	2.0			0.0		0.0		2.0
Bottom	2.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0		0.0		0.0
pH																
Surface	8.0	8.1	8.3	8.2	8.5	8.0	8.1	8.2	8.4	8.2	7.8	8.1		8.0		8.4
30	7.9	8.1	8.0	8.1	8.5	8.0	8.0	8.0	8.4			8.1		7.9		8.3
Bottom	7.8	7.9	7.8	7.7		7.8	7.8	7.5	7.5	8.1	7.8	7.7		7.5		7.9
Secchi Disc, feet																
		11	15								18					

1952
STATION 1 (42°12.0', 81°54.0')

Depth in Feet	1952														
	6/4	6/12	6/17	6/27	7/5	7/7	7/14	7/16	7/22	7/24	7/29	8/7	8/19	8/30	9/5
							Water Temperature, °C								
Surface	14.7	11.7	19.3	18.3	21.9	21.9	23.4	22.9	24.3	20.3	24.1	23.4	23.3	23.6	21.5
15	13.9	10.8	16.4	17.9	21.1	21.2	23.2	21.8	22.5	20.1	23.2	23.0	23.1	23.3	20.6
30	13.0	10.5	13.0	15.5	19.9	20.2	21.3	19.6	11.9	11.4	22.2	22.5	22.6	22.9	19.7
Bottom	9.9	10.5	10.5	12.7	12.7	13.0	10.8	11.0	10.2	10.2	10.8	11.4	16.1	12.5	12.6
							Dissolved Oxygen, ppm								
Surface	9.2	10.1	6.2	8.9	8.5		7.4		7.9	7.8	8.0	8.7	8.7	9.6	9.7
30	9.7	8.6	10.4	9.0	8.7		8.0	7.8	7.6	7.8	7.8	8.6	8.5	9.4	9.2
Bottom	7.8	9.9	9.7	8.8	7.5		7.0	6.9	7.7	6.9	7.0	8.4	8.4	6.7	8.6
							Free Carbon Dioxide, ppm								
Surface	3.2	3.3	2.0	0.0	0.0		0.0	1.0	2.3	4.3	0.0		0.0	0.0	4.0
30	2.0	3.0	1.3	1.3	0.0		2.0	3.3	2.0	2.6	2.0	0.0	0.0	0.0	5.3
Bottom	2.0	2.0	1.7	2.0	2.3		3.0	2.6	5.0	4.3	3.6	0.0	0.0	3.6	6.9
							Methyl Orange Alkalinity, ppm $CaCO_3$								
Surface	114	114	118	117	105		103	103	108	96	98	105	102	105	99
30	110	118	114	111	106		109	97	109	101	98	99	109	108	91
Bottom	112	116	110	109	115		123	69	108	102	109	99	101	113	94
							Phenolphthalein Alkalinity, ppm $CaCO_3$								
Surface	0.0	0.0	0.0	0.0	1.5		3.0	0.0	0.0	0.0	1.5	0.0	7.5	4.5	0.0
30	0.0	0.0	0.0	0.0	2.5		0.0	0.0	0.0	0.0	0.0		8.0	5.0	0.0
Bottom	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0		7.0	0.0	0.0
							pH								
Surface	8.1	7.8	8.2	8.0	8.0		8.2	8.0	8.0	7.3	7.7	8.3	8.4	8.4	7.8
30	7.9	7.6	8.0	8.2	8.2		8.1	7.9	7.8	7.8	8.2	8.0	8.2		7.8
Bottom	7.8	7.7	7.7	7.9	7.9		7.9	7.0	7.7	7.4	7.5	8.3	8.2	8.0	7.8

1953
STATION 1 (42°12.0', 81°54.0')

Depth in Feet	1953															
	6/2	6/10	6/15	6/29	7/3	7/9	7/15	7/30	8/6	8/13	8/24	8/25	8/31	9/1	9/8	9/14
								Water Temperature, °C								
Surface	13.5	15.4	16.0	21.0	18.4	20.7	23.6	22.8	22.4	23.1	23.3	23.9	25.3	26.3	21.5	17.1
15	12.5	14.7	15.4	19.8	17.4	19.1	23.4	22.8	22.4	22.5	23.0	23.3		25.4	21.5	16.9
30	12.0	14.0	14.8	18.8	16.2	14.2	20.3	16.2	22.2	22.5	22.8	23.0	22.9	23.5	21.5	16.7
Bottom	11.8	10.6	11.4	11.8	11.4	11.3	11.5	11.1	20.4	14.5	12.6	12.7	12.7	13.5	13.2	15.3
								Dissolved Oxygen, ppm								
Surface	10.5	9.4	9.6	8.9	8.9	8.9	8.7	8.6	8.3	8.7	8.6	8.6	7.9	8.3	7.5	6.5
30	10.2	9.7	9.1	9.0	8.2	8.7	8.4	7.1	10.3	8.4	8.4		8.0		7.5	6.1
Bottom	9.2	9.8	9.1	8.8	8.4	8.4	7.5	7.2	10.8	5.2	3.5	3.2	2.2	2.0	2.4	5.1
								Free Carbon Dioxide, ppm								
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0
30		0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0		0.0		1.0	3.0
Bottom	0.0	0.0	0.0	0.0	0.0	2.0	4.0	3.0	0.0	3.0	0.7	5.5	0.5	6.0	7.0	4.0
								Phenolphthalein Alkalinity, ppm $CaCO_3$								
Surface	8.0	5.0	5.0	2.8	2.7	2.0	3.0	4.0	4.8	4.5	5.0	5.5	4.0	4.2	0.8	0.0
30		2.5	2.5	2.0	1.8	0.0	1.5	0.0	3.2	5.5	2.7		3.3		0.0	0.0
Bottom	8.0	2.5	2.5	0.7	1.1	0.0	1.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
								pH								
Surface	8.0	7.8	8.0	8.0	8.1	8.0			8.4	8.4	8.4	8.4	8.4	8.4	7.8	7.5
30	8.2	7.8	7.9	8.1	8.0	7.6			8.4	8.4	8.4		8.4		7.8	7.5
Bottom	8.1	7.8	7.8	7.6	8.0	7.8			7.8	7.6	7.5	7.6	7.4	7.5	7.5	7.4
								Secchi Disc, feet								
	2	12	26	27	27	16	21	14	10	26	34	31	15		13	7

1947 and 1948
STATION 2 (42° 07.2', 81° 53.9')

Depth in Feet	1947						1948								
	7/28	8/8	8/13	8/21	9/13	9/27	4/23	6/4	6/19	7/8	7/31	8/13	8/26	8/30	9/9
Water Temperature, °C															
Surface	22.1	24.1	25.0	26.8	23.8	17.3	4.6	14.7	15.5	18.6	22.7	20.9	25.1	24.4	22.7
30	20.9	17.2	23.4	18.8	23.7	16.9	4.4	10.7	14.2	18.2	22.7		23.2	23.8	23.1
45	20.9	11.5	12.2	12.6	23.4	16.6				17.0	22.5	20.7	22.0	22.4	23.0
Bottom	10.5	11.0	10.8	11.9	12.7	14.5	4.4	10.2	12.6	11.0	11.3	11.1	11.4	15.2	17.0
Mean	18.6	16.9	18.3	19.0	21.2	16.4	4.5	11.7	14.8	17.2	22.1		21.0	23.1	21.6
Mean of Epilimnion	21.2	23.4	24.4	25.4	23.7					18.1	22.6		23.7	23.7	
Dissolved Oxygen, ppm															
Surface								9.8	11.0	9.4	8.2	8.2	7.5	7.9	8.0
30	8.5	7.0		7.4	7.3	6.3		9.8	11.2		8.1	8.2	8.0	3.1	8.0
45	7.9					6.5		7.7	10.2	9.5	8.0		6.2	3.1	8.1
Bottom		7.0		6.9						6.6	7.8	5.0			
Free Carbon Dioxide, ppm															
Surface				0.0	0.0				0.0		0.0	0.0	0.0	0.0	0.0
30					0.0				0.0		0.0	0.0	0.0	0.0	0.0
45					0.0				0.0		0.0	1.3	0.0	0.0	0.0
Bottom					6.4				0.0	1.8	0.0	1.3	22.1	46.2	1.8
Methyl Orange Alkalinity, ppm Ca CO_3															
Surface				115	96	100		106	105	98	104	102	110	104	103
30					97	100			105		98	104	107	104	102
45				150		100			96	98	102	106	109	106	105
Bottom				150	100	100		107	117	106	98	108	117	106	93
Phenolphthalein Alkalinity, ppm $CaCO_3$															
Surface				1.5	3.0			5.0	4.0	2.4	4.0	4.0	9.0	7.0	4.0
30					3.0				14.0		3.0	2.0	11.0	6.0	6.0
45					3.0				4.0	3.6	3.6	0.0	2.0	3.0	6.0
Bottom					0.0			1.0	2.0	0.0	2.0	0.0	0.0	0.0	0.0
pH															
Surface	8.0	8.1		8.2	8.0	8.0		8.3	8.4	8.4	8.0	8.2	8.3	8.3	8.5
30	8.0				7.9	7.9			8.5		8.4	8.2	8.0	8.3	8.5
45		7.4		7.4					8.4	8.4	8.0	7.3	8.0	8.3	8.5
Bottom	7.5			7.3	7.4	7.4		7.9	8.3	7.7	8.0	7.4	7.2	7.3	7.5
Secchi Disc, feet															
	25	19	25		25	11									

1949
STATION 2 (42° 07.2', 81° 53.9')

Depth in Feet	1949											
	6/10	6/19	6/27	7/6	7/12	7/20	7/28	8/4	8/10	8/23	9/7	9/15
						Water Temperature, °C						
Surface	15.2	20.4	23.2	26.2	22.0	24.0	25.5	25.0	26.0	23.2	20.7	19.2
30	14.6	16.4	16.3	20.1	21.8	22.8	24.5	24.2	24.7	23.0	20.8	19.4
45	14.4	12.7	12.4	12.4	21.5	22.3	22.5	23.6	24.1	22.4	20.6	19.2
Bottom	11.3	11.1	10.0	11.2	12.2	12.4	11.4	12.5	12.0	12.5	19.4	18.4
Mean	14.3	15.9	16.5	19.4	20.4	21.1	21.6	22.3	22.9	21.3	20.0	19.2
Mean of Epilimnion			22.6	25.6	21.7	22.9	24.4	24.3	25.7	23.0		
						Dissolved Oxygen, ppm						
Surface	9.5	10.2	9.6	8.3	8.8	8.6	9.2	8.7	8.3	8.6	8.1	8.1
30		9.5	9.3	8.5	8.0	8.4	8.4	8.8	9.1	7.5	8.2	7.4
45		9.0	9.9	8.0	8.0	8.5	8.6	8.4	8.7	8.2	8.2	8.0
Bottom	10.0	9.0	9.1	7.6	7.0	6.0	6.0	4.5	5.1	2.4	8.1	6.4
						Free Carbon Dioxide, ppm						
Surface		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
30		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
45		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bottom		0.0	1.9	0.9	2.6	2.2	4.0	5.0	4.4	5.3	1.8	0.0
						Methyl Orange Alkalinity, ppm $CaCO_3$						
Surface		124	124	112	112	120	112	116	112	116	104	100
30		124	116	128	116	116	116	114	114	118	105	100
45		124	114	128	116	118	112	114	114	118	105	100
Bottom		120	111	96	114	112	116	110	108	114	104	100
						Phenolphthalein Alkalinity, ppm $CaCO_3$						
Surface		5.0	6.0	4.0	3.0	4.0	5.0	5.0	2.5	5.0	2.0	2.0
30		6.0	5.0	4.0	3.0	3.0	4.0	4.0	2.5	5.0	2.5	2.0
45		4.0	4.0	0.0	3.0	3.0	3.0	3.0	2.0	3.0	2.0	2.0
Bottom		5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
						pH						
Surface		7.8	8.0	8.1	8.2	8.3	8.2	8.3	8.3	8.5	8.4	8.4
30		7.9	8.1	8.2	8.2	8.2	8.2	8.2	8.2	8.5	8.3	8.1
45		7.8	8.0	7.8	8.0	8.2	8.0	8.2	8.2	8.2	8.2	8.1
Bottom		7.8	7.8	7.7	7.6	7.6	7.6	7.3	7.3	7.3	8.1	8.0
						Secchi Disc, feet						
	27	43	47	22	33	27	25					

1950
STATION 2 (42° 07.2', 81° 53.9')

Depth in Feet	1950											
	5/26	6/7	6/15	6/25	7/5	7/14	7/18	7/26	8/8	8/24	9/1	10/1
						Water Temperature, °C						
Surface	11.9	16.3	17.2	21.2	20.1	21.4	21.6	20.8	21.9	21.9	22.4	19.4
30	8.6	12.2	12.6	17.2	19.7	20.7	21.0	20.5	21.5	21.6	22.4	18.0
45	5.6	6.6	8.5	15.0	14.7	20.6	20.7	20.4	21.3	21.5	22.4	17.8
Bottom	5.4	6.5	6.6	10.3	10.4	11.3	10.2	10.3	10.0	12.4	12.7	17.5
Mean	8.1	10.9	12.5	16.6	17.4	19.6	19.2	19.2	19.1	21.1	21.6	18.2
Mean of Epilimnion		13.9	15.4	18.3	19.8	20.8	21.2	20.5	21.6	21.6	22.4	
						Dissolved Oxygen, ppm						
Surface	12.7	11.2	10.2	10.0	8.2	8.4		8.4	8.1	8.2	8.3	7.6
30		11.2	10.6	10.0	7.4	8.6		8.5	8.1	8.6	8.0	7.4
45		11.8		10.1	6.1	9.1		8.0	7.7	8.7	7.8	7.1
Bottom	12.0	11.8	10.1	9.4	6.9	7.6		7.3	6.1	3.8	3.8	7.1
						Free Carbon Dioxide, ppm						
Surface	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0
30		0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0
45		0.9	1.3		1.8	0.4		0.0	0.9	0.0	0.0	0.9
Bottom	0.9	1.3	0.9		4.4	4.4		1.8	3.5	6.6	6.2	0.9
						Methyl Orange Alkalinity, ppm $CaCO_3$						
Surface	112	110	102	117	110	104		111	101	105	103	101
30		105	97	112	108	103		110	102	103	102	100
45		120	100	118	110	109		108	102	103	104	102
Bottom	115	107	100	116	98	107		110	103	105	106	102
						Phenolphthalein Alkalinity, ppm $CaCO_3$						
Surface	3.0	1.0	2.0		2.0	1.0		3.0	2.5	3.0	2.5	2.0
30		1.5	2.0		1.0	1.0		3.0	2.5	3.0	2.5	1.0
45		0.0	0.0		0.0	0.0		2.0	0.0	2.0	2.5	0.0
Bottom	0.0	0.0	0.0		0.0	0.0		0.0	0.0	0.0	0.0	0.0
						pH						
Surface	8.1	8.1	8.2	8.2	8.0			8.2	8.4	8.4	8.4	8.1
30		8.2	8.2	8.2	8.0	8.2		8.2	8.4	8.4	8.4	8.0
45		8.1	7.6	8.0	7.9	8.0		8.0	7.9	8.2	8.4	7.9
Bottom	7.9	8.0	7.6	7.6	7.8	7.7		7.4	7.3	7.3	7.2	7.8
						Secchi Disc, feet						
		27	19	17								23

1951
STATION 2 (42° 07.2', 81° 53.9')

Depth in Feet	1951													
	5/23	5/30	6/12	6/21	6/28	7/2	7/12	7/18	7/23	8/2	8/8	8/24	8/28	9/2
Water Temperature, °C														
Surface	9.1	13.0	15.8	18.5	19.1	19.3	19.9	21.9	21.6	22.3	21.3	21.3	21.8	21.3
30	9.0	11.3		17.1	17.7	18.8	18.9	20.0	21.2	22.1	21.2	21.3	21.5	21.3
45	8.6	8.0		12.4	17.1	8.7	14.7	14.9	16.0	21.2	21.2	21.3	21.4	21.3
Bottom	6.6	7.9		9.2	10.2	8.5	10.4	9.5	11.0	12.7	10.2	10.5	10.8	11.3
Mean	8.6	10.4		14.7	15.9	15.5	16.9	18.1	18.7	20.6	19.8	18.8	20.6	20.6
Mean of Epilimnion				17.1	18.0	19.0	19.3	20.8	21.4	22.1	21.3	21.3	21.6	21.3
Dissolved Oxygen, ppm														
Surface	10.2	11.9	10.9	10.7	10.8	9.8	9.1	9.2	9.0		8.1	8.6	8.9	
30	11.4	11.6	11.2	10.6	10.2	9.7	9.6	9.5	9.1		8.9	8.8	9.2	
45	12.3	12.4	10.5	10.9	9.2	9.3	9.7	9.0	8.8		8.7	7.8	9.1	
Bottom	11.1	11.3	10.6	10.5	9.2	9.2	9.0	8.7	8.3		7.4	5.6	4.7	
Free Carbon Dioxide, ppm														
Surface	7.1	6.2	5.4	2.2	3.2	6.2	3.5	0.9	2.6	0.0	0.0	0.0	0.0	
30	5.3		5.4	1.8	1.8	5.3	3.5	2.2	3.5	0.0	0.0	0.0	0.0	
45			5.4	2.6	3.1	5.3	6.1	3.5	3.5		0.0	0.0	0.0	
Bottom			5.4	4.4	3.6	7.1	5.3	4.4	4.4	3.1	4.8	1.8	3.1	
Methyl Orange Alkalinity, ppm $CaCO_3$														
Surface	100	120	126	107	108	101	104	104	106	104	104	104	102	
30	120		120	107	107	103	104	104	102	103	103	105	105	
45			122	109	110	105	105	106	108		102	105	105	
Bottom			108	109	109	104	105	108	109	105	104	107	108	
Phenolphthalein Alkalinity, ppm $CaCO_3$														
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	3.0	5.0	3.5	
30	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0	2.5	3.0	
45			0.0	0.0	0.0	0.0	0.0	0.0	0.0		1.0	2.0	1.5	
Bottom			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
pH														
Surface	7.8	7.8	7.8	7.7	7.9	7.6	8.0	8.2	8.3	8.0	8.0	8.0	8.3	
30	7.8		7.9	7.8	7.9		7.7	7.9	8.1	8.3	8.0	7.9	8.4	
45			8.0	7.7	7.6		7.7	7.7	8.0		7.9	8.0	8.4	
Bottom	7.8		8.0	7.6	7.5	7.8	7.7	7.5	7.7	7.5	7.6	7.5	7.9	
Secchi Disc, feet														
	13	11			40		23	29	22				26	

1952
STATION 2 (42° 07.2', 81° 53.9')

Depth in Feet	1952										
	6/4	6/12	6/17	6/27	7/5	7/14	7/29	8/8	8/19	8/30	9/5
					Water Temperature, °C						
Surface	13.7	14.9	18.5	18.7	21.9	23.1	25.2	23.7	24.3	23.1	22.0
30	12.4	13.4	14.2	18.4	20.0	22.1	24.4	23.2	23.5	22.5	21.8
45	8.8	11.4	9.4	14.5	19.7	21.3	24.1	23.0	23.4	21.9	21.6
Bottom	8.7	9.7	9.1	9.8	11.2	11.4	11.2	11.9	11.4	11.5	11.2
Mean	11.3	13.0	13.4	16.4	18.6	21.2	21.2	21.7	21.3	19.4	19.3
Mean of Epilimnion			16.5	19.6	20.3	22.4	24.3	23.3	23.6	22.6	21.8
					Dissolved Oxygen, ppm						
Surface	10.5	9.8	8.8	8.3	9.1	8.6	6.6	8.8	9.0		9.7
30	10.7	10.0	6.4	9.1	9.1	8.5	6.7	8.0	9.2	8.9	9.8
45	10.6	10.0	5.7	8.9	8.7	8.7	7.3	8.3	8.9	8.9	9.6
Bottom	11.0	10.4	5.8	8.6	8.1	8.3	6.9	5.9	8.3	4.7	9.5
					Free Carbon Dioxide, ppm						
Surface	1.3	2.0		0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.3
30	2.0	1.3	0.7	3.3	0.0	2.3	8.6	3.0	0.0	0.0	1.0
45	2.5	1.7	1.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	1.7
Bottom	1.5	2.3	1.7	1.7	4.0	2.0	1.7	3.3	2.3	0.0	4.0
					Methyl Orange Alkalinity, ppm $CaCO_3$						
Surface	114	106	105	108	97	107	101	97	102	105	81
30	109	112	112	109	102	109	100	97	104	104	95
45	115	114	115	111	104	107	100	104	84	103	94
Bottom	113	112	108	114	110	107	96	107	113	107	89
					Phenolphthalein Alkalinity, ppm $CaCO_3$						
Surface	0.0	0.0	0.0	0.0	6.0	0.0	2.0	3.5	6.5	6.0	0.0
30	0.0	0.0	0.0	0.0	3.5	0.0	0.0	0.0	5.5	11.5	0.0
45	0.0	0.0	0.0	0.0	1.5	4.0	2.0	4.0	10.0	6.5	0.0
Bottom	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	0.0
					pH						
Surface	8.0	8.0	7.4	8.4	8.2	8.0	8.2	8.2	8.3	8.4	7.9
30	8.2	7.9	7.8	8.0	8.1	7.9		7.5	8.4	8.4	8.2
45	7.8	7.9	8.0	7.9	7.9	8.0	7.9	8.4	8.0	8.2	8.4
Bottom	8.0	7.9	7.4	7.9	7.6	7.9	8.0	7.4	8.0	7.8	8.3
					Secchi Disc, feet						
	15	28	48	28	42	28	28		28	25	19

1947 and 1948
STATION 3 (42°01.2', 81°52.8')
STATION 4 (41°56.4', 81°52.8')
STATION 5 (41°51.6', 81°52.8')

Depth in Feet	Station															
	3	4	5	3	4	5	3	4	5	3	4	5	3	4	5	5
	1947						1948									
	8/13	8/13	8/13	9/27	9/27	9/27	4/23	4/23	4/23	6/4	6/4	6/4	7/8	7/8	7/8	8/13
Water Temperature, °C																
Surface	25.0	25.9	26.7	16.8	18.4	18.6	4.2	4.5	4.6	16.0	16.6	16.4	20.6	20.2	20.0	21.5
30	23.4	23.2	23.7	16.4	18.4	18.4	4.2	4.3	4.3		12.3		19.0		19.3	
45	21.8	20.7	21.5	16.2	17.7	18.0				10.6		12.1	16.9			21.1
60	11.0	10.5	11.3	16.0	11.7	11.0				10.5			10.2	16.4	17.4	11.2
Bottom	10.7	10.5	10.7	14.7	11.0	11.0	4.2	4.2	4.2	10.5	10.7	10.2	9.6	11.3	11.6	10.9
Mean	20.0	20.1	20.8	16.4	17.0	16.8	4.2	4.3	4.3	11.7	12.4	12.1	16.4	17.4	17.8	18.6
Mean of Epilimnion	23.7	23.5	24.0		18.1	18.4							19.5	18.6	19.1	21.3
Dissolved Oxygen, ppm																
Surface									11.6			8.3	8.9		9.2	8.5
30									9.0				11.6		9.0	
45																8.1
60															6.7	
Bottom									7.6				11.6			3.4
Free Carbon Dioxide, ppm																
Surface									0.0		0.0	0.0	0.0		0.0	0.0
30												0.0	0.0		0.0	0.0
45											0.0	0.0	0.0		0.0	0.0
60									0.0		0.0		1.3		0.9	1.8
Methyl Orange Alkalinity, ppm $CaCO_3$																
Surface									100		105	102	96		99	102
30												104	99		100	104
45											103	104	100		99	104
60									100		105	108	108		106	108
Bottom											104	104				104
Phenolphthalein Alkalinity, ppm $CaCO_3$																
Surface									4.0		5.0	4.0	5.0		4.0	5.0
30												1.6	4.4		7.2	5.0
45											3.0	3.0	6.8		6.0	4.0
60									4.0		1.0		0.0		0.0	0.0
Bottom												3.0				
pH																
Surface									8.0	8.1	8.1	8.1	8.4		8.4	8.4
30										8.1	8.1	8.1	8.4		8.4	8.4
45										8.1		8.1	8.2		8.4	8.4
60									8.0	8.1	8.1	7.9	7.4		7.6	7.2
Bottom																7.4

1949 and 1950
STATION 3 (42°01.2', 81°52.8')
STATION 4 (41°56.4', 81°52.8')
STATION 5 (41°51.6', 81°52.8')

Depth in Feet	Station											
	3	4	5	3	4	5	3	4	5	3	4	5
	1949						1950					
	8/4	8/4	8/4	8/23	8/23	8/23	6/8	6/8	6/8	7/26	7/26	7/26
Water Temperature, °C												
Surface	24.8	24.3	24.0	23.6	23.8	23.7	17.1	16.3	16.0	20.7	20.7	21.0
30	23.8	23.8	23.8	22.9	23.4	23.1	12.5	12.2	12.7			
45	23.5	23.5	22.4	22.6	23.1	23.0	9.2	9.1	6.4	20.2	20.3	20.3
60	11.5	11.0	11.1	13.2	12.5	12.1	6.4	6.2	6.3	8.8	14.5	9.1
Bottom	11.2	11.0	10.8	12.3	11.8	11.6	6.3	6.2	6.3	8.7	8.6	9.0
Mean	20.1	21.0	19.6	21.3	21.3	20.1	10.9	10.6	10.7	18.0	18.1	17.1
Mean of Epilimnion	23.9	23.8	23.7	23.1	23.4	23.1	13.8	20.4	13.4	20.5	13.6	20.6
Dissolved Oxygen, ppm												
Surface	8.7	8.8	8.7				11.5	9.4	10.5	8.4	9.4	9.7
30	8.8	8.9	8.8				11.6	11.1	11.3	9.4	9.4	9.5
45	8.8	8.7	8.9				11.7	11.3	10.4	9.6	9.6	9.4
60	6.4	6.2	6.9				10.8	11.1	10.1	8.3	8.2	8.3
Bottom	6.2	6.4	6.7				11.4	11.6	10.1	7.9	8.3	7.9
Free Carbon Dioxide, ppm												
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
30	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
45	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.9	0.0	0.0	0.0
60	5.0	2.0	3.0	1.8	2.6	2.2	1.3	1.3	2.2	1.8	1.8	2.6
Bottom	5.5	4.0	4.0	4.5	4.0	3.5	2.2	1.8	3.5	3.5	2.6	2.6
Methyl Orange Alkalinity, ppm $CaCO_3$												
Surface	116	116	114	116	116	120	100	105	109	109	110	110
30	114	114	114	118	116	116	97		110	109	110	108
45	114	116	114	116	116	118	97	105	108	109	110	108
60	110	112	110	114	114	114	96	107	97	110	108	108
Bottom	108	110	110	116	116	112	102	100	104	110	108	106
Phenolphthalein Alkalinity, ppm $CaCO_3$												
Surface	5.0	5.0	5.0	5.0	5.0	5.0	2.0	2.0	4.0	6.0	6.0	6.0
30	2.0	5.0	4.0	5.0	4.0	4.0	4.0	5.0	3.0	4.0	6.0	6.0
45	2.0	4.0	4.0	4.0	4.0	3.0	0.0	5.0	0.0	4.0	6.0	6.0
60	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bottom	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
pH												
Surface	8.2	8.2	8.2	8.5	8.5	8.5	7.9	8.1	8.1	8.2	8.2	8.2
30	8.2	8.2	8.2	8.5	8.5	8.5	8.0	8.0	8.0	8.2	8.2	8.2
45	8.2	8.2	8.1	8.4	8.5	8.2	7.9	7.6	7.8	8.0	8.2	8.2
60	7.4	7.5	7.5	7.7	7.5	7.8	7.7	7.6	7.6	7.7	7.4	7.5
Bottom	7.3	7.4	7.3	7.4	7.3	7.5	7.7	7.6	7.6	7.4	7.4	7.4
Secchi Disc, feet												
	26	27	25		26	22	26	23				

1951
STATION 3 (42°01.2', 81°52.8')
STATION 4 (41°56.4', 81°52.8')
STATION 5 (41°51.6', 81°52.8')

Depth in Feet	Station 3	4	5	3	4	5	3	4	5	3	4	5	3	4	5
	1951														
	5/30	5/30	5/30	6/12	6/12	6/12	6/28	6/28	6/28	7/18	7/18	7/18	8/28	8/28	8/28
Water Temperature, °C															
Surface	11.6	11.7	11.8		15.5	15.8	20.5	20.7	20.2	23.0	23.6	24.2	22.3	24.6	24.1
30	9.7	9.9	10.9		13.7	14.3	17.0	17.5	18.0	21.3	19.4	18.6	21.5	22.1	21.6
45	9.3	9.8	10.8		10.1	10.4	16.5	12.1	12.6	18.5	16.6	16.3	21.4	21.6	21.4
60	6.3	6.4	6.9		6.8	6.8	7.7	7.2	7.2	7.9	8.1	8.0	10.2	20.8	9.6
Bottom	6.3	6.4	6.9		6.8	6.7	7.7	7.1	7.2	7.8	8.0	7.8	10.2	10.2	9.4
Mean	9.3	9.1	9.7		11.2	11.5	14.8	13.7	12.4	16.7	16.0	16.2	19.7	20.4	19.2
Dissolved Oxygen, ppm															
Surface	11.4	11.6	10.7	11.7	11.5	11.0	10.0	9.8	10.0	9.2	9.3	9.1	9.0	9.2	9.1
30	11.3	12.2	10.6	12.2	10.3	10.8	10.5	10.1	9.8	9.5	9.7	9.3	9.0	9.3	8.9
45	12.3	12.6	10.6	12.5	12.3	11.9	10.0	10.5	9.9	9.6	9.7	9.3	9.0	9.0	
60	10.9	12.1	9.6	11.4	11.4	11.9	10.2	10.4	9.5		8.9	8.9	3.2		
Bottom	10.9	11.6	8.0	10.9	11.0	10.1	10.0	10.3	10.0	8.5	8.2	9.6	2.1	4.9	5.0
Free Carbon Dioxide, ppm															
Surface	10.6	10.6	6.2	6.2	4.4	5.3	5.3	3.5	3.5	0.9	3.1	3.1	0.0	0.0	
30					4.4	4.4	5.3	3.5	4.4	2.2	1.3	4.8	0.0	0.0	0.0
45					4.4		5.3	3.5	5.3	3.0	3.1	2.2	0.0	0.0	
60					4.4		3.5	5.3	5.3		4.4	5.7	2.6	2.6	
Bottom			7.0		5.3	7.1	3.5	7.0	5.3	4.4	5.3	4.4	4.4	6.6	0.9
Methyl Orange Alkalinity, ppm $CaCO_3$															
Surface	118	116	120	108	110	108	106	110	110	104	104	102	104	104	
30					104	106	120	106	107	106	104	106	108	104	106
45					108		106	108	110	106	104	103	105	102	
60					112		112	109	110		106	104	105	103	
Bottom			110		110	112	112	109	109	108	108	105	105	104	106
Phenolphthalein Alkalinity, ppm $CaCO_3$															
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	1.0	
30					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	1.0	3.5
45					0.0		0.0	0.0	0.0	0.0	0.0	0.0	3.0	2.0	
60					0.0		0.0	0.0	0.0		0.0	0.0	0.0	0.0	
Bottom					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
pH															
Surface	7.8	7.8	7.8	8.0	7.9	6.8	7.9	8.2	8.2	8.0	8.0	7.9	8.4	8.0	
30					7.5	7.9	7.7	8.0	7.9	7.8	8.0	7.7	8.3	8.2	8.4
45					7.7		7.6	7.9	7.6	7.5	7.7	7.8	8.3	8.3	
60					7.7		7.7	7.9	7.6		7.3	7.4	7.4		
Bottom			7.7		7.6	7.6	7.6	7.6	7.6	7.3	7.3	7.3	7.4	7.5	7.5
Secchi Disc, feet															
	17	18	18				26	30	30	30	45	37	26	31	32

1950 and 1951
STATION 6 (41° 43.8', 81° 55.8')
STATION 7 (41° 34.8', 82° 04.2')
STATION 8 (41° 27.6', 82° 22.8')
STATION 9 (41° 30.0', 82° 40.8')
STATION 14 (41° 53.4', 82° 24.6')
STATION 15 (41° 58.2', 82° 15.0')
STATION 16 (42° 01.8', 82° 04.2')

Depth in Feet	Station												
	14	15	16	14	15	16	6	7	8	9	14	15	16
	1950										1951		
	6/25	6/25	6/25	7/30	7/30	7/30	7/26	7/26	7/26	7/26	7/23	7/23	7/23
Maximum	45	58	65	38	63	69	66	52	42	28	50	65	65
Water Temperature, °C													
Surface	22.4	21.8	21.8	22.4	22.4	22.4	21.2	20.5	24.7	26.3	24.1	22.4	22.2
30	8.7	18.2	18.5	17.7	20.8	20.9	20.5	19.5	21.3		9.6	20.8	21.2
45	8.5	8.5	16.9		19.7	20.2	19.4	19.1			9.4	18.4	15.2
60			8.8		12.5	8.2	9.1					9.3	9.2
Bottom	8.5	8.2	8.7	14.0	8.4	8.1	9.1	12.2	18.6	20.9	9.3	9.2	9.1
Dissolved Oxygen, ppm													
Surface	9.7		9.3	8.3	8.3	8.4	9.5	9.2	8.2	11.3	9.0	9.2	9.1
30	6.7	9.7	9.8	7.5	8.6	8.7	9.4	8.1	7.9		7.9	9.3	9.1
45	6.3	9.0	9.5		8.1	8.6	9.2				7.8	8.4	8.4
60			8.5		6.1	8.6	8.2					7.8	8.0
Bottom	6.3	9.1		7.5		6.9		4.7	7.6	7.7			
Free Carbon Dioxide, ppm													
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	2.7	1.8
30	7.9	0.0	0.0	2.6	0.0	0.0		0.0	0.9		3.6	1.4	2.7
45	13.0	8.8	0.0		0.0	0.0	1.3	0.9			4.5	3.2	3.6
60			16.7		4.4	1.8	1.8					5.4	4.5
Bottom	13.0	16.7		2.6		2.6		2.2	1.8	0.9			
Methyl Orange Alkalinity, ppm $CaCO_3$													
Surface	113	116	112	105	106	104	108	108	108	106	102	104	106
30	115	115	119	107	106	106		109	108		105	104	108
45	125	113	116		105	105	110	111			108	106	106
60			118		107	104	114					106	112
Bottom	125	132		107		100		111	108	108			
Phenolphthalein Alkalinity, ppm $CaCO_3$													
Surface	0.0	2.0	2.0	2.5	2.5	2.5	2.5	2.0	3.0	3.0	0.0	0.0	0.0
30	0.0	1.0	0.0	0.0	2.0	2.0		1.5	0.0		0.0	0.0	0.0
45	0.0	0.0	0.0		2.0	2.0	0.0	0.0			0.0	0.0	0.0
60			0.0		0.0	2.0	0.0					0.0	0.0
Bottom	0.0	0.0		0.0		0.0		0.0	0.0	0.0			
pH													
Surface	8.0	8.2	8.2	8.3	8.4	8.5	8.2	8.2	8.2	8.5	8.3	8.1	8.3
30	7.9	8.2	8.2	7.5	8.2	8.2	8.2	8.2	7.6		7.9	8.2	8.2
45	7.4	7.7	8.2		8.2	8.2	8.0	7.8			7.8	8.2	7.6
60			7.4		7.3	7.5	7.5					7.4	7.6
Bottom	7.4	7.5		7.5		7.4		7.4	7.6	7.8			
Secchi Disc, feet													
	30	7									10	27	30

1950 and 1951
STATION 18 (42° 12.6', 81° 32.4')
STATION 20 (42° 16.8', 81° 10.8')
STATION 22 (42° 27.6', 80° 49.2')
STATION 23 (42° 28.8', 80° 31.8')

Depth in Feet	Station															
	18	20	22	23	18	20	22	23	18	20	22	23	18	20	22	23
	1950								1951							
	7/5	7/5	7/5	7/6	8/8	8/8	8/8	8/11	7/2	7/2	7/2	7/3	8/8	8/8	8/8	8/9
Maximum	73	65	58	48	71	67	60	52	73	70	65	55	73	73	61	50
Water Temperature, °C																
Surface	19.7	20.2	18.6	18.0	22.1	22.5	22.4	21.1	18.8	19.0	19.6	20.8	21.9	21.8	21.2	21.9
30	16.4	16.7	15.4	13.6	20.9	21.2	20.8	18.0	18.5	18.5	19.2	19.5	21.5	21.5	20.5	20.3
45	7.8	16.0	7.3	8.5	20.5	21.0	20.4	15.2	7.7	8.3	8.6	5.9	21.4	21.4	15.8	16.1
60	7.6	8.1			10.7	20.8	13.6		7.6	8.3	8.5		10.9	10.9	11.2	
Bottom	7.4	8.0	7.2	8.3	10.3	14.2	13.6	14.7	7.6	8.3	8.5	5.8	10.8	10.8	11.2	14.7
Dissolved Oxygen, ppm																
Surface	8.2	9.1	8.2	10.0	8.7		9.7	8.4	9.8	9.6	9.5	9.3	8.3	8.8	9.0	9.0
30	8.4	8.6	8.4	9.5	8.3	7.2	9.9	9.0	9.7	9.6	9.5	9.5	8.6	8.8	9.0	
45	8.7	9.0	8.0		8.2	6.5	9.7	8.8	10.7	9.8	9.5	12.1	8.9	8.8	8.0	
60	8.1	9.0			7.3	4.8	8.3		9.5	9.6	9.5		6.2	6.6	7.9	
Bottom	7.5	8.8	8.0	9.8	7.3	4.4	8.3	8.5	9.1	9.0		12.3	6.3	6.3	7.9	8.5
Free Carbon Dioxide, ppm																
Surface	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	3.5	3.5	3.5	8.0	0.9	2.6	0.0
30	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	5.3	4.4	4.4	5.3	0.0	0.0	1.3	0.0
45		0.0	2.6	1.3	0.0	0.0	0.0	0.9	5.3	4.4	4.4	7.0	13.2	0.0	3.5	
60					2.6	0.0	1.8		5.3	6.2	5.3		6.2	3.1	4.0	
Bottom			2.6	1.8	3.5	1.8	1.8	1.3		5.3		7.0	5.3	3.5	4.0	1.3
Methyl Orange Alkalinity, ppm $CaCO_3$																
Surface	100	106	104	105	98	99	104	104	101	104	104	102	104	104	102	106
30	100	110	110	108	98	100	103	105	101	101		104	103	105	103	105
45	105	100	107	105	101	101	101	103	100		102	105	104	105	105	
60	130	100			108	99	100		100	102	103		108	106	106	
Bottom	120	78	103	106	104	105	100	104		102		106	107	106	106	108
Phenolphthalein Alkalinity, ppm $CaCO_3$																
Surface	2.0	2.0	2.5	2.5	2.5	2.0	2.5	2.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	3.0
30	1.0	2.0	0.0	2.0	1.5	1.0	3.0	1.0	0.0	0.0		0.0	2.0	3.0	0.0	3.0
45	0.0	1.0	0.0	0.0	1.5	2.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	
60	0.0	0.0			0.0	2.0	0.0		0.0	0.0	0.0		0.0	0.0	0.0	
Bottom	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0		0.0	0.0	0.0	0.0	0.0
pH																
Surface	8.1	8.2	8.0	8.2	8.4	8.4	8.4	8.4	7.9	7.9	7.9	7.9	7.9	7.9	8.2	
30	8.0	8.1	8.0	8.0	8.3	8.2	8.4	8.2	8.0	7.8	7.9	8.0		8.2	7.8	8.2
45	7.6	8.0	7.8	7.7	8.2	8.2	8.3	7.8	7.8	7.6	7.7	7.8	7.8	8.0	7.5	
60	7.5	7.6			7.3	8.2	7.6		7.6	7.5	7.6		7.5	7.7	7.4	
Bottom	7.4	7.4	7.8	7.6	7.3	7.4	7.6	7.7		7.4		7.6	7.6	7.7	7.4	8.1
Secchi Disc, feet																
									23	23	21	19				

1950 and 1951
STATION 24 (42°27.6', 79°54.0')
STATION 25 (42°31.8', 80°02.4')

Depth in Feet	Station 24				Depth in Feet	Station 25	
	7/6/50	8/10/50	7/3/51	8/9/51		7/7/50	8/10/50
Maximum	197	180	197	190		112	127
			Water Temperature, °C				
Surface	17.9	20.1	20.2	21.1	Surface	17.8	20.8
30	13.8	20.1	17.4	20.9	30	13.0	18.4
60	7.8	14.5	5.2	10.2	45	10.6	15.5
90	5.7	6.1	4.2	6.9	60	9.7	11.3
120	4.3	4.0	4.0	5.5	75	8.2	6.5
150	4.0	4.0	4.0	4.6	90	4.2	4.4
Bottom	3.9	4.0	4.0	4.4	Bottom	4.0	4.1
			Dissolved Oxygen, ppm				
Surface		8.8	9.2	8.9	Surface	8.1	9.0
30	9.4		9.5	9.0	30	8.7	9.2
60	9.2		12.3	9.0	45	8.7	9.0
90	8.2		12.6	9.9	60	8.3	9.6
120	9.1		12.8	11.4	75	8.0	9.3
150	9.1	8.2	12.0	11.3	90	9.0	9.5
Bottom	8.2		11.2	10.0	Bottom	8.0	8.7
			Free Carbon Dioxide, ppm				
Surface	0.0	0.0	5.3	0.0	Surface	0.0	0.0
30	0.0		7.0	0.0	30	1.3	0.0
60	1.8		7.0	2.6	45	1.3	0.4
90	1.3		5.3	1.7	60	1.3	1.8
120	2.6		6.1	1.3	75	2.2	1.8
150	2.6	1.8	5.3	0.9	90	3.1	1.8
Bottom	2.2		5.3	1.3	Bottom	2.6	2.6
			Methyl Orange Alkalinity, ppm $CaCO_3$				
Surface	110	104	104	106	Surface	112	102
30	108		104	106	30	110	100
60	106		104	106	45	119	102
90	104		103	106	60	110	101
120	110		103	106	75	113	105
150	111	105	106	105	90	112	105
Bottom	106		109	106	Bottom	114	110
			Phenolphthalein Alkalinity, ppm $CaCO_3$				
Surface	2.0	1.5	0.0	4.0	Surface	3.0	2.5
30	1.0		0.0	3.0	30	0.0	2.0
60	0.0		0.0	0.0	45	0.0	0.0
90	0.0		0.0	0.0	60	0.0	0.0
120	0.0		0.0	0.0	75	0.0	0.0
150	0.0	0.0	0.0	0.0	90	0.0	0.0
Bottom	0.0		0.0	0.0	Bottom	0.0	0.0
			pH				
Surface	8.2	8.2	8.0	8.2	Surface	8.2	8.4
30	8.1		7.8	8.2	30	7.9	8.3
60	7.7		7.6	7.9	45	7.9	7.9
90	7.6		7.7	8.1	60	7.8	7.6
120	7.8		7.6	8.0	75	7.8	7.5
150	7.8	7.5	7.5	7.9	90	7.7	7.5
Bottom	7.6		7.5	7.9	Bottom	7.7	7.4

GEOFISICA INTERNACIONAL

REVISTA DE LA UNIÓN GEOFÍSICA MEXICANA, AUSPICIADA POR EL INSTITUTO DE GEOFÍSICA DE LA UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

G. I. RODEN

SOBRE LA CIRCULACION PRODUCIDA POR EL VIENTO EN EL GOLFO DE TEHUANTEPEC Y SUS EFECTOS SOBRE LAS TEMPERATURAS SUPERFICIALES

ON THE WIND-DRIVEN CIRCULATION IN THE GULF OF TEHUANTEPEC AND ITS EFFECTS UPON SURFACE TEMPERATURES

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SOBRE LA CIRCULACION PRODUCIDA POR EL VIENTO EN EL GOLFO DE TEHUANTEPEC Y SUS EFECTOS SOBRE LAS TEMPERATURAS SUPERFICIALES *

G. I. Roden

RESUMEN

Se investiga la relación entre los vientos y las temperaturas de la superficie del mar en el Golfo de Tehuantepec. Se encuentra que las bajas temperaturas de invierno están relacionadas con la divergencia inducida por el viento en el transporte de las masas, cuya magnitud es de unos 0.02 g cm^{-2} seg^{-1} durante una galerna de invierno. Un análisis espectral de las anomalías de vientos y temperaturas en períodos de 10 días, indica que las anomalías en cuadrados adyacentes de 2 grados de latitud y longitud, son coherentes y casi simultáneas. Existe una relación más bien débil e inversa entre las anomalías del viento y la temperatura.

INTRODUCCION

El Golfo de Tehuantepec está situado directamente al sur del Istmo de Tehuantepec, una interrupción importante en la cordillera llamada Sierra Madre en el sur de México. En su punto más estrecho, el Istmo tiene unos 220 Km de un lado al otro. Hay aquí una interrupción de unos 40 Km en la cordillera; la maxima elevación en este lugar es de unos 250 m. Las ondas frías del norte que pasan a través del Istmo y llegan a una atmósfera más cálida, producen vientos "de descenso" de violencia particular. Esos vientos, conocidos de ordinario como "*Tehuantepequeros*" son más frecuentes en invierno y se sienten a varios centenares de kilómetros hacia el sur. El efecto de esos vientos sobre la superficie del océano es doble: mueven el agua hacia el sur, originando un arrastre de ella desde los lados y desde abajo y causan una mezcla considerable a lo largo del eje del viento. Estos últimos dos procesos llevan a un abatimiento considerable de la temperatura superficial del Golfo de Tehuantepec, que puede ser varios grados más baja que la observada en cualquier parte de la región mar afuera del sur de México y América Central.

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G. I. Roden

ABSTRACT

The relation between winds and sea surface temperatures in the Gulf of Tehuantepec is investigated. The low winter temperatures are found to be related to the wind induced mass transport divergence, the magnitude of which is about 0.02 g $cm^{-2}sec^{-1}$ during a winter gale. A spectral analysis of ten-day temperature and wind anomalies indicates that anomalies in adjacent two degree squares of latitude and longitude are coherent and almost simultaneous. There exists a rather weak and inverse relation between temperature and wind anomalies.

INTRODUCTION

The Gulf of Tehuantepec lies directly south of the Isthmus of Tehuantepec, a major break in the Sierra Madre mountain range of Southern Mexico. At the narrowest point the Isthmus is about 220 Km across. Here, there is a gap of about 40 Km in the cordillera, the maximum elevation at this point being roughly 250 m. Cold waves from the north which pass through the Isthmus into the warmer atmosphere beyond produce *fall* winds of particular violence. These winds, commonly known as *Tehuantepecers*, occur most frequently in winter and are felt several hundred kilometers to the southward. The effect of these winds upon the ocean surface is twofold; they move the water to the southward causing entrainment of the water from the sides and from below, and they cause considerable mixing along the wind axis. The last two processes lead to a substantial lowering of the surface temperatures in the Gulf of Tehuantepec which may be several degrees lower than observed elsewhere in the region off southern Mexico and Central America.

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Apenas existen investigaciones que se refieran a las condiciones meteorológicas y oceanográficas del Golfo de Tehuantepec. Hurd (1929) dio una descripción bastante detallada de los vientos. Las corrientes superficiales durante un "*Tehuantepequero*" fueron descritas vívidamente por la U. S. Hydrographic Office (1951): "La furia del norte arroja el agua fuera del Golfo hacia el sureste y cuando el agua baja en la parte superior, hay una corriente violenta a lo largo de cada ribera, hacia el norte, para llenar el vacío. Cuando el norte amaina o cesa de soplar, el agua que se ha represado fluye hacia atrás golfo arriba y una cantidad extra se precipita hacia el sur a lo largo de cada ribera. Este hecho se ha observado hacia el oeste hasta el Río Verde y hacia el este tan lejos como Champerico..." La descripción citada muestra claramente que el arrastre del agua tiene lugar durante el período de vientos fuertes y que después que el viento ha dejado de soplar, hay un reajuste al estado inicial. Se ha informado que la corriente costera hacia el norte durante la galerna adquiere una velocidad de 2 nudos y que la velocidad de la corriente costera hacia el sur después de aquella, es de 0.6 nudos; ambos datos vienen de Sacrificios. La distribución de las variables hidrográficas en el Golfo, según expediciones recientes, fue estudiada por Blackburn (MS). Una de las características interesantes fue que las temperaturas superficiales más bajas no ocurrieron en las cabeceras del Golfo, sino a alguna distancia hacia el sur.

Cuando las condiciones que producen un "*Tehuantepequero*" se extienden suficientemente hacia el sur en el Golfo de México, se encuentran también otras áreas de vientos de alta velocidad mar afuera de las costas de América Central, notablemente en el Golfo de Papagayo y en el Golfo de Fonseca. Los vientos en esas regiones, conocidos localmente como "*Papagayos*", ocurren en una escala relativamente pequeña y tienen sobre la temperatura superficial un efecto similar a los "*Tehuantepequeros*".

There are only few investigations dealing with the meteorological and oceanographical conditions in the Gulf of Tehuantepec. A rather detailed description of the winds is given by Hurd (1929). The surface currents during a *Tehuantepecer* are quite vividly described by the U. S. Hydrographic Office (1951); "The fury of the norther blows the water out of the gulf to the southward and, as the waters lower at the head, there is a rush along each shore to the northward to supply or fill the vacancy. When the norther moderates or ceases to blow, the water that was banked up, as it were, flows back up the gulf, and an extra amount rushes out along each shore to the southward. This fact has been observed as far west as Rio Verde and eastward as far as Champerico..." The above description clearly shows that entrainment of water takes place during the period of high winds and, after the wind has ceased to blow, there is readjustment to the initial state. The speed of the coastal nortward setting current during the gale is reported to be 2 knots and the speed of the coastal southward setting current after the gale 0.6 knots; both reported off Sacrificios. The distribution of hydrographic variables in the Gulf, based on recent cruises, was studied by Blackburn (MS). One of the interesting features was that the lowest surface temperatures did not occur at the head of the Gulf, but some distance to the southward.

When the conditions inducing the *Tehuantepecer* extend sufficiently far southward into the Gulf of Mexico, other areas of high wind velocity are found off the coast of Central America, notably in the Gulf of Papagayo and in the Gulf of Fonseca. The winds in these regions, locally known as *Papagayos* occur on a relatively small scale and have a similar effect upon the surface temperature as the *Tehuantepecers*.

DATOS

Los datos de vientos y temperaturas superficiales en las estaciones costeras se obtuvieron del Servicio Meteorológico Mexicano (1928-1941) y del U. S. Coast and Geodetic Survey (1956, 1960) respectivamente. La exactitud de las observaciones individuales de temperatura en la costa se acerca a 0.3° C y de las observaciones individuales del viento a casi un 10% de la velocidad del viento. Las observaciones de temperatura y de velocidad del viento tomadas mar afuera a bordo de barcos mercantes, se obtuvieron del U. S. Weather Bureau (datos no publicados) para el período entre Enero de 1949 y Junio de 1957. La exactitud de las observaciones individuales no es muy grande: probablemente de ± 0.5° C para la temperatura y de ± 20% de la velocidad para las observaciones del viento. Una inspección cuidadosa de los registros lleva a la conclusión de que la calidad de las observaciones de temperatura es razonablemente buena, mientras que la calidad de

DATA

Winds and sea surface temperatures at coastal stations were obtained from the Servicio Meteorologico Mexicano (1928-1941) and the U. S. Coast and Geodetic Survey (1956, 1960), respectively. The accuracy of individual coastal temperature observations is about ± 0.3 C and of individual wind observations about ± 10% of the wind speed. Offshore sea surface temperature and wind observations, taken aboard merchant ships, were obtained from the U. S. Weather Bureau (unpublished) for the period January 1949 to June 1957. The accuracy of individual observations is not great, probably ± 0.5 C for temperature and ± 20% of the wind speed for wind observations. A careful inspection of the records leads to the conclusion that the quality of temperature observations is reasonably good, whereas the quality of the wind observations is only moderate. The individual observations were combined and

las observaciones de viento es solamente moderada. Las observaciones individuales se combinaron y promediaron en cuadros de dos grados de latitud y longitud y en períodos de diez días y de un mes. El número de observaciones incluido en cada promedio de diez días varía generalmente entre 10 y 30. Las medias para cuadros de un grado de las temperaturas de superficie en Enero y Agosto se obtuvieron de la U. S. Hydrographic Office (datos no publicados) y del U. S. Bureau of Commercial Fisheries (1960).

averaged over two degree squares of latitude and longitude and over periods of ten days and one month. The number of observations entering each ten-day average varies generally between 10 and 30. Mean one degree square sea surface temperatures for February and August were obtained from the U. S. Hydrographic Office (unpublished) and the U. S. Bureau of Commercial Fisheries (1960). Monthly five degree sea surface temperatures off southern

TABLA I

Velocidades máximas y medias mensuales del viento en Coatzacoalcos, Ver., Salina Cruz, Oax. y en el Golfo de Tehuantepec, según el Servicio Meteorológico Mexicano (1928-1947) y el U. S. Weather Bureau (inéditos).

TABLE I

Monthly mean and maximum wind velocities at Coatzacoalcos, Ver., Salina Cruz, Oax., and in the Gulf of Tehuantepec, after Servicio Meteorológico Mexicano (1928-1947) and U. S. Weather Bureau (unpublished).

Unidades en / All units in m sec^{-1}

Mes / Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Años de registro / Years of record
						Coatzacoalcos, Ver.							
V media / mean	8.6	7.7	5.7	5.5	5.0	4.5	6.2	3.5	4.3	4.0	9.7	9.5	3
V max	29.5	28.5	21.3	17.3	20.0	16.7	22.0	17.3	19.0	19.0	29.0	30.0	3
						Salina Cruz, Oax.							
V media / mean	8.7	8.7	8.3	7.8	6.7	3.9	5.2	4.9	4.1	6.0	8.3	8.4	12
V max	28.2	26.3	27.2	26.5	21.7	18.1	19.8	19.9	19.6	24.5	27.0	26.4	12
	Golfo de Tehuantepec (Norte)					14-16 N 94-96 W			(North) Gulf of Tehuantepec				
V media / mean	7.6	6.3	4.8	4.2	4.4	4.4	5.0	4.6	4.	7.6	8.4	8.1	8
V max	18.6	22.2	18.6	16.6	13.6	15.2	12.4	11.2	14.7	16.8	20.0	25.4	6
	Golfo de Tehuantepec (Sur)					12-14 N 94-96 W			(South) Gulf of Tehuantepec				
V media / mean	6.2	5.4	3.7	3.8	3.4	4.2	4.4	3.7	4.6	6.5	7.1	6.4	8
V max	15.2	13.9	13.4	13.0	11.2	13.1	11.3	9.7	12.9	13.9	15.7	16.9	6
	Golfo de Tehuantepec (Oeste)					14-16 N 96-98 W			(West) Gulf of Tehuantepec				
V media / mean	4.2	3.5	3,4	3.4	3.7	4.1	4.3	4.0	4.5	4,3	4.0	3.7	8
V max	15.6	9.8	13.2	10.1	12.9	12.4	12.6	10.2	13.1	14.7	15.9	15.4	6
	Golfo de Tehuantepec (Este)					12-14 N 92-94 W			(East) Gulf of Tehuantepec				
V media / mean	3.4	2.7	2.7	2.8	3.2	3.8	4.1	3.4	3.8	4.5	3.4	3.4	8
V max	9.1	8.7	10.9	10.6	10.2	10.7	11.6	11.6	13.0	14.4	12.7	11.3	6

Los datos de temperatura mensuales para cuadros de cinco grados, tomadas mar afuera de las costas de México y América Central, se obtuvieron de las publicaciones del Observatorio de Kobe, de la Marina Imperial (1921-1938). Las medias de las corrientes de deriva de barcos para el período 1885-1933, se obtuvieron de la U. S. Hydrographic Office (1947). Es de notar que los promedios que allí se reportan se basan en observaciones de corrientes hechas a velocidades del viento menores de 12 m sec^{-1}.

Mexico and Central America were taken from publications by the Imperial Marine Observatory Kobe (1921-1938). Mean one degree ship drift currents for the period 1885-1933 were obtained from the U. S. Hydrographic Office (1947). It is noteworthy that the averages reported therein are based on current observations made at wind speeds less than 12 m sec^{-1}.

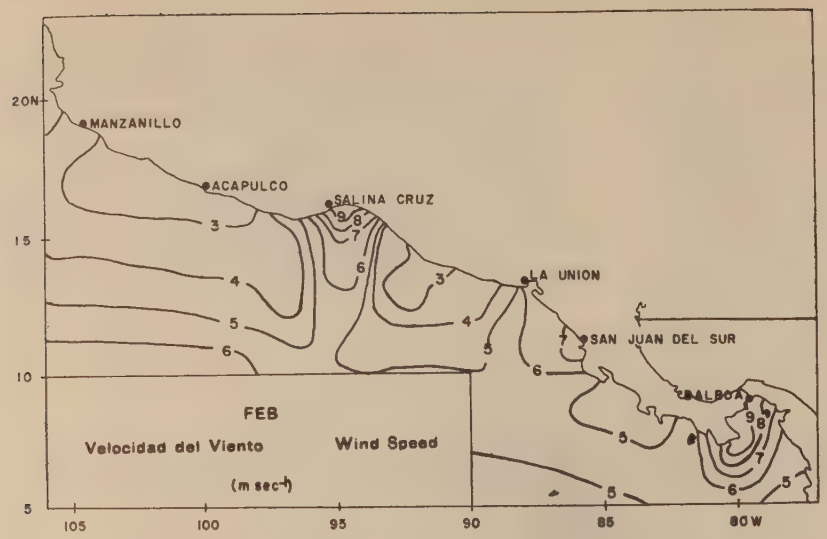


Fig. 1a. Velocidad media del viento, corrientes de deriva de barcos y temperaturas de la superficie del mar para el mes de Febrero, basadas en datos del U. S. Weather Bureau (inéditos), U. S. Hydrographic Office (1947 e inéditos) y Bureau of Commercial Fisheries (inéditos).

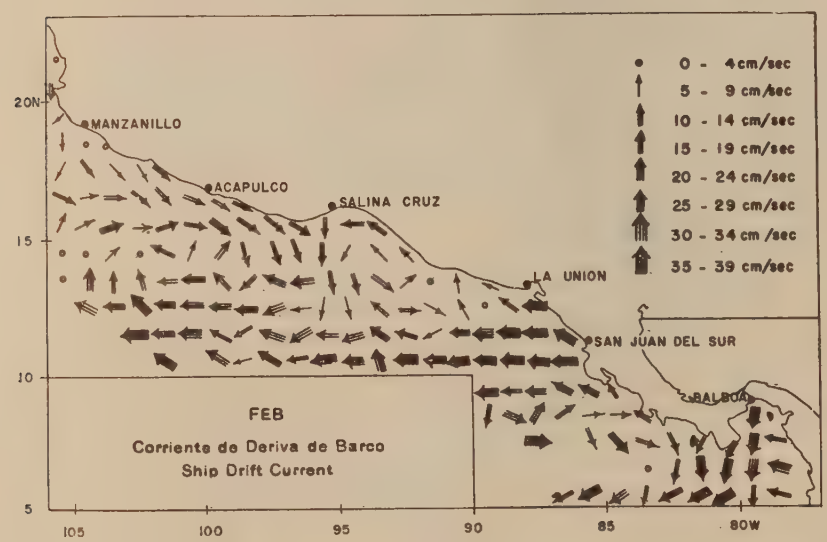
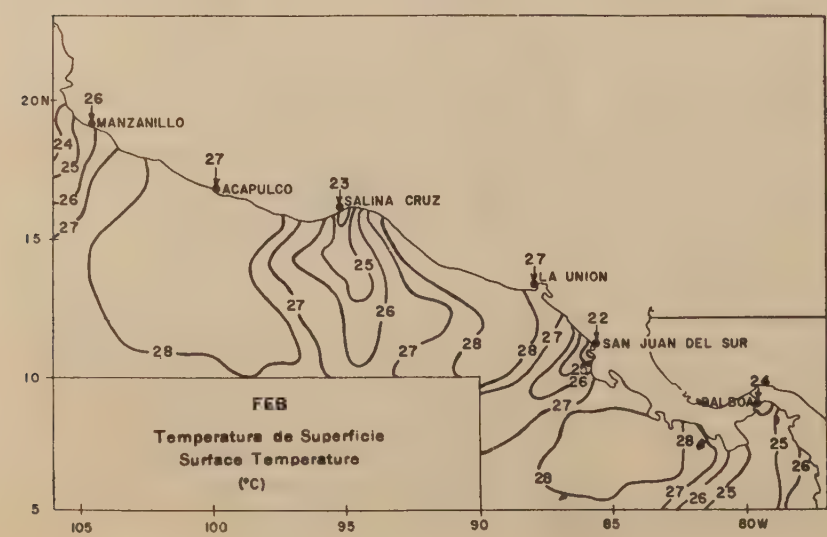


Fig. 1a. Mean wind speed, ship drift currents and sea surface temperatures for the month of February, based on material from the U. S. Weather Bureau (unpublished), the U. S. Hydrographic Office (1947 and unpublished) and the Bureau of Commercial Fisheries (unpublished).



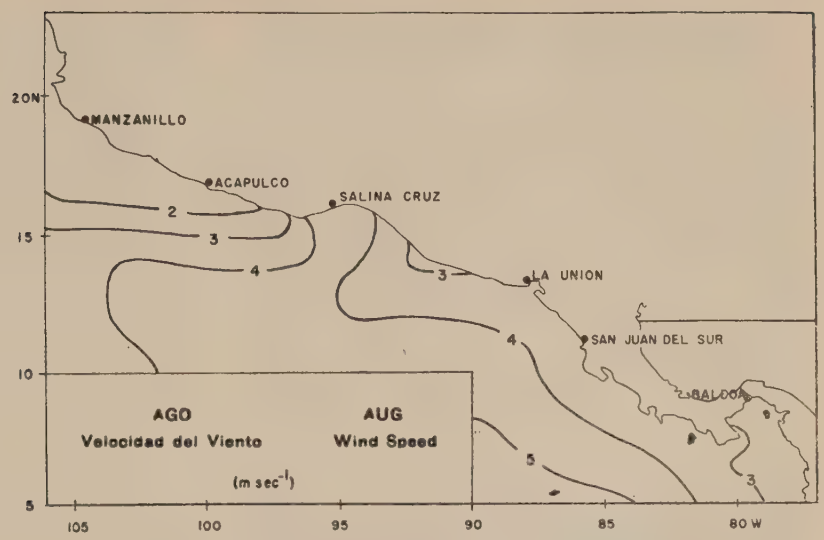


Fig. 1b. Velocidad media del viento, corrientes de deriva de barcos y temperaturas de la superficie del mar para el mes de Agosto, basadas en datos del U. S. Weather Bureau (inéditos), U. S. Hydrographic Office (1947 e inéditos).

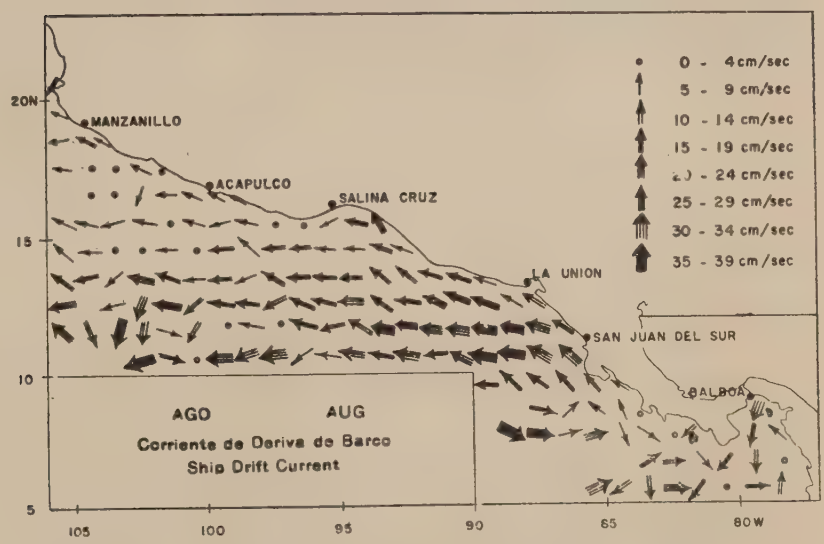
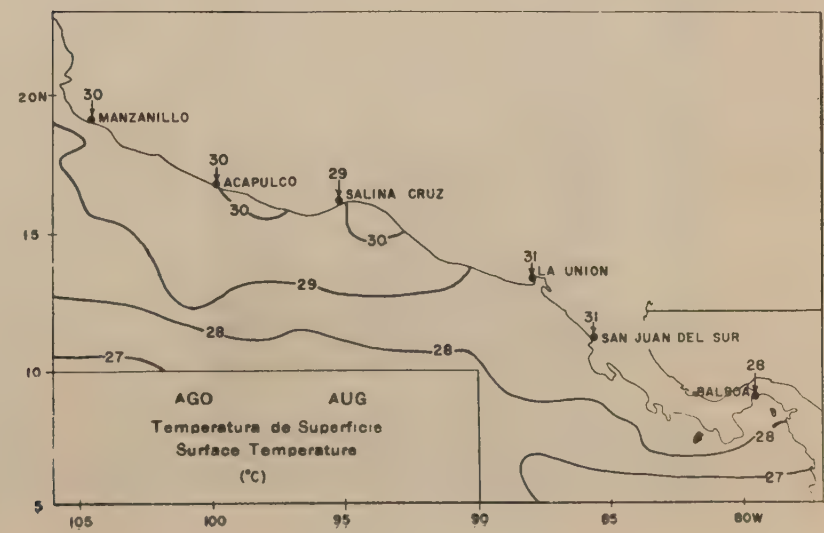


Fig. 1b. Mean wind speed, ship drift currents and sea surface temperatures for the month of August, based on material from the U. S. Weather Bureau (unpublished), and the U. S. Hydrographic Office (1947 and unpublished).



VARIACIONES ESTACIONALES DE LAS CONDICIONES OCEANOGRAFICAS Y METEOROLOGICAS

Las estaciones en el Golfo de Tehuantepec pueden dividirse en una seca y generalmente ventosa de Noviembre a Abril y una lluviosa y usualmente en calma desde Mayo hasta Octubre. Durante la estación ventosa (Figs. 1a y 1b) una faja de vientos de alta velocidad se extiende hacia el sur desde el Istmo de Tehuantepec, en una longitud de unos 500 Km; su anchura es de unos 200 Km y las velocidades mayores tienen lugar en la extremidad norte del Golfo. Ahí la dirección del viento no se desvía mucho del norte. En la región de los vientos fuertes se ve que la corriente va hacia el sur con una velocidad media de unos 20 cm seg^{-1}.

THE SEASONAL VARIATION OF OCEANOGRAPHIC AND METEOROLOGICAL CONDITIONS

The seasons in the Gulf of Tehuantepec can be devided into a dry and generally windy season from November to April and a rainy and usually calm season from May to October. During the windy season (Figs. 1a and 1b) a belt of high wind speeds extends southward from the Isthmus of Tehuantepec for about 500 Km; its width is about 200 Km and the highest speeds occur at the northern end of the Gulf. The wind direction there does not vary much from north. In the region of strong winds the current is seen to set toward the south with an average speed of about 20 cm sec^{-1}. Along the coast the mean currents set toward Salina

TABLA 2

Temperaturas medias mensuales y medias máximas y mínimas de la superficie del mar en Coatzacoalcos, Ver., Salina Cruz, Oax., San Juan del Sur, Nicaragua y en el Golfo de Tehuantepec, según el U. S. Coast and Geodetic Survey (1956, 1960) y el U. S. Weather Bureau (inéditos).

TABLE 2

Monthly mean and mean maximum and minimum sea surface temperatures at Coatzacoalcos, Ver., Salina Cruz, Oax., San Juan del Sur, Nicaragua and in the Gulf of Tehuantepec, after U. S. Coast and Geodetic Survey (1956, 1960) and U. S. Weather Bureau (unpublished).

Unidades en / All units in °C

Month / Mes	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Años de registro / Years of record
						Coatzacoalcos, Ver.							
media / mean	23.1	24.2	26.2	27.9	29.0	29.0	27.5	28.0	27.1	25.6	24.7	23.3	13
max	25.1	26.7	28.9	30.0	31.2	31.1	29.8	29.3	29.1	27.4	22.8	25.9	13
min	21.2	22.2	23.6	25.3	26.5	26.9	25.8	26.2	24.9	24.9	22.4	21.2	13
						Salina Cruz, Oax.							
media / mean	23.0	22.7	24.8	26.2	27.9	28.4	28.6	28.8	28.1	26.4	24.1	23.3	4
max	26.1	25.4	28.1	28.8	30.2	29.7	30.3	30.3	30.4	30.0	29.2	28.1	4
min	18.9	20.0	18.9	22.4	23.9	25.8	26.8	27.2	27.0	22.8	18.1	18.7	4
						San Juan del Sur, Nicaragua							
media / mean	24.3	21.9	22.4	25.0	27.0	28.5	27.7	28.8	30.8	29.9	27.8	25.9	4
max	27.3	26.8	27.3	29.6	30.4	31.0	30.4	32.9	33.8	34.9	32.3	31.5	4
min	19.6	18.2	19.3	21.1	21.1	24.9	24.3	24.6	26.0	23.5	22.7	21.1	4
	Golfo de Tehuantepec (Norte)					14-16 N 94-96 W			(North) Gulf of Tehuantepec				
media / mean	25.5	25.9	27.2	28.9	29.7	29.6	29.3	29.8	29.4	28.0	26.3	26.0	8
max	28.7	29.3	29.8	31.4	31.4	31.2	30.8	31.5	31.3	30.7	30.6	29.8	6
min	19.0	21.3	22.8	25.6	27.4	27.2	27.3	27.8	27.6	22.7	19.0	19.8	6
	Golfo de Tehuantepec (Sur)					12-14 N 94-96 W			(South) Gulf of Tehantepec				
media / mean	25.3	26.4	28.1	29.9	30.0	29.6	29.1	29.5	29.2	27.6	26.6	25.9	8
max	28.3	28.5	30.3	31.1	31.8	30.8	30.4	30.9	30.8	30.2	29.7	29.3	6
min	21.6	22.2	24.8	26.0	27.1	27.7	27.1	27.9	27.0	24.0	21.8	21.3	6
	Golfo de Tehuantepec (Oeste)					14-16 N 96-98 W			(West) Gulf of Tehuantepec				
media / mean	27.3	27.4	28.2	28.8	29.6	29.5	29.3	29.9	29.5	28.8	28.4	27.3	8
max	30.3	29.7	30.2	30.9	31.6	31.3	30.9	31.5	31.5	30.2	31.0	30.0	6
min	20.7	22.1	25.0	25.3	27.8	26.2	27.7	27.7	26.9	24.2	24.1	21.9	6
	Golfo de Tehuantepec (Este)					12-14 N 92-94 W			(East) Gulf of Tehuantepec				
media / mean	26.7	27.4	28.5	29.5	29.9	29.5	29.2	29.4	29.3	28.1	28.1	27.7	8
max	29.4	29.8	30.1	31.8	31.7	31.1	30.9	31.3	31.5	30.3	30.4	29.8	6
min	23.2	22.8	25.4	27.1	28.0	27.5	26.4	27.4	27.0	24.9	23.2	23.7	6

A lo largo de la costa las corrientes medias van hacia Salina Cruz para reemplazar el agua que se ha movido. La circulación local de Tehuantepec se observa hacia el sur hasta las latitudes 12° N o 13° N, donde encuentra la Corriente Ecuatorial del Norte. Las temperaturas superficiales del mar son bajas donde las velocidades del viento son altas y también en las regiones inmediatamente adyacentes, lo cual indica que hay una difusión de agua fría hacia las áreas vecinas. Es de notar que la anchura del área de agua fría es algo mayor al sur del Golfo de Tehuantepec que dentro del mismo; esta característica sugiere que el efecto de surgencia en el Golfo está contrarrestado parcialmente por arrastres laterales de agua caliente.

Durante el verano los vientos son generalmente débiles y soplan de una dirección oriental. Ocasionalmente se observan vientos de alta velocidad durante el paso de huracanes, que ocurren con una frecuencia de unos dos por mes en el punto culminante de la estación en Septiembre. Las corrientes superficiales se establecen hacia el oeste y el noroeste, con velocidades de unos 15 cm seg^{-1}. Las temperaturas superficiales varían mayormente entre 28° C y 30° C y son las más altas en el Pacífico tropical oriental, excepto el Golfo de California (Roden y Groves, 1959).

Cruz to replace the water that has been moved away. The local Tehuantepec circulation is felt southward as far as latitude 12 N or 13 N, where it meets the North Equatorial Current. The sea surface temperatures are low everywhere the wind speeds are high and also in immediately adjacent regions, which indicates that outward diffusion of cold water into neighboring areas takes place. It is noteworthy that the width of the cold water area is somewhat larger south of the Gulf of Tehuantepec than inside the Gulf; this feature suggests that the upwelling effect in the Gulf is partly counteracted by lateral entrainment of warm water.

During the summer season the winds are generally weak and blow from an easterly direction. High wind speeds are occasionally observed during the passage of hurricanes which occur with a frequency of about two per month at the height of the season in September. The surface currents set toward the west and northwest with speeds of about 15 cm sec^{-1}. The sea surface temperatures vary mostly between 28° C and 30° C and are the highest in the eastern tropical Pacific, excepting the Gulf of California (Roden and Groves, 1959).

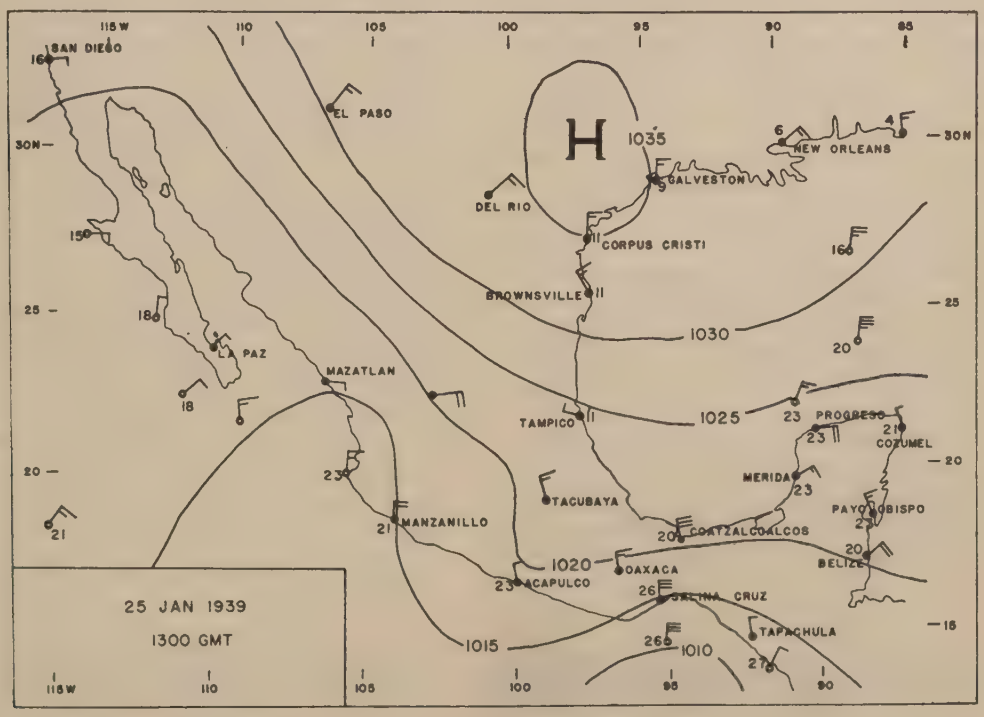


Fig. 2. Una situación típica del tiempo que produce vientos fuertes en los Golfos de México y Tehuantepec. Las isobaras están representadas por líneas continuas y otros números indican las temperaturas del aire en la superficie del mar (según U. S. Weather Bureau, 1939).

Fig 2. A typical weather situation leading to strong winds in the Gulfs of Mexico and Tehuantepec. Isobars are represented by solid lines, other numbers refer to air temperatures at the sea surface (after U. S. Weather Bureau, 1939).

La variación anual de vientos y temperaturas se muestra en las Tablas 1 y 2. Se observa que el promedio de las velocidades máximas durante la estación de "*Tehuantepequeros*" varía alrededor de 25 m seg^{-1} y que los vientos en Coatzacoalcos, en el extremo norte del Istmo, no difieren mucho de los de Salina Cruz, en el extremo sur. La más alta velocidad del viento observada en Salina Cruz fue de 36 m seg^{-1} en Marzo de 1931. En el Golfo de Tehuantepec la velocidad del viento disminuye lentamente hacia el sur y rápidamente hacia el oriente y el occidente. La media de las mínimas de las temperaturas superficiales del mar en el punto culminante de la estación ventosa es de unos 18° C y a 19° C en la parte norte del Golfo y algo más alta en otros lugares. La temperatura más baja registrada en Salina Cruz es de 16.7° C y valores igualmente bajos han sido reportados por barcos mercantes. Es interesante hacer notar que las temperaturas mínimas en Coatzacoalcos, en el extremo norte del Istmo, están entre 20° C y 21° C o sea unos cuatro grados más altas que en Salina Cruz. Las temperaturas máximas en mar abierto en el Golfo varían entre 29° C y 30° C y en algunas áreas costeras entre 31° C y 43° C.

Una situación meteorológica típica que lleva a la producción de vientos fuertes en el área de Tehuantepec, se muestra en la Fig. 2. La característica más saliente del mapa meteorológico es un anticiclón continental bien desarrollado con su centro sobre la parte media de Texas que se extiende bastante hacia el sur dentro del Golfo de México. Esto conduce a un influjo de aire frío que viene desde las llanuras centrales y del noreste de los Estados Unidos. El desbordamiento del aire frío hacia el sur es detenido usualmente por las altas montañas del México meridional. Las ondas frías pasan al Océano Pacífico únicamente a través del Istmo de Tehuantepec y de la región del Lago de Nicaragua. Los vientos en esas regiones son fuertes, en parte debido a la tendencia que tienen las corrientes de aire de fluir alrededor de las montañas y amontonarse a través de sus interrupciones y en parte debido a la energía liberada cuando el aire frío fluye por sobre el aire caliente, más allá de la interrupción en la montaña (Godske *et al.*, 1957). Los "*Tehuantepequeros*" y "*Papagayos*" pertenecen a la clase de *Vientos de descenso,* cuya teoría ha sido desarrollada recientemente por Gutman y Frankl (1960). La intensidad de esos vientos depende de la elevación del Istmo, del espesor del frente frío y de la diferencia en los gradientes del lapso entre el aire frío y el aire caliente desplazado.

The annual variation of winds and temperatures is shown in Tables 1 and 2. It is seen that the mean maximum wind velocities during the *Tehuantepecer* season vary around 25 m sec^{-1} and that the winds at Coatzacoalcos at the northern end of the Isthmus are not very different from those at Salina Cruz at the southern end. The highest wind speed observed at Salina Cruz was 36 m sec^{-1} in March 1931. In the Gulf of Tehuantepec the wind speeds diminish slowly toward the south and rapidly toward the east and west. The mean minimum sea surface temperatures at the height of the windy season are about 18° C to 19° C in the northern part of the Gulf and somewhat higher elsewhere. The lowest temperature recorded at Salina Cruz is 16.7° C; similar low values have been reported from merchant ships. It is of interest to note that the minimum temperatures at Coatzacoalcos at the northern end of the Isthmus are between 20° C and 21° C, or about 4° C higher than at Salina Cruz. The maximum temperatures in the open Gulf vary between 29° C and 30° C and in localized coastal areas between 31° C and 34° C.

A typical weather situation leading to strong winds in the Tehuantepec area is shown in Fig. 2. The outstanding feature on the weather map is a well developed continental anticyclone with its center over central Texas and extending far southward into the Gulf of Mexico. This leads to an influx of cold air from the plain states and from the northeast. The southward spread of the cold air is usually halted by the high mountains of southern Mexico. Only across the Isthmus of Tehuantepec and the Nicaragua lake district do cold waves pass into the Pacific Ocean. The winds in these regions are strong partly because of the tendency of air currents to flow around mountains and to crowd through mountain gaps, and partly because of the energy released when cold air overflows the warm air beyond the mountain gap (Godske *et al.*, 1957). The *Tehuantepecers* and *Papagayos* belong to the class of *fall winds,* the theory of which has recently been developed by Gutman and Frankl (1960). The intensity of these winds is dependent upon the elevation of the isthmus, the thickness of the cold front and the difference in lapse rates between the cold air and the displaced warm air.

ALGUNOS ASPECTOS HIDRODINAMICOS DE LA CIRCULACION DE TEHUANTEPEC PRODUCIDA POR EL VIENTO

Para investigar la circulación producida por el viento en el Golfo de Tehuantepec, supóngase un sistema de coordenadas rectas y exprésense las ecuaciones de movimiento y continuidad según

SOME HYDRODINAMIC ASPECTS OF THE WIND DRIVEN TEHUANTEPEC CIRCULATION

In order to investigate the wind driven circulation in the Gulf of Tehuantepec assume a right-handed coordinate system, and let the equations of motion and continuity be given by

$$0 = -\frac{\partial p}{\partial x} + f\rho v + \frac{\partial \tau_{zx}}{\partial z}$$

$$0 = -\frac{\partial p}{\partial y} - f\rho u + \frac{\partial \tau_{zy}}{\partial z} \qquad (1)$$

$$0 = \frac{\partial \rho u}{\partial x} + \frac{\partial \rho v}{\partial y} + \frac{\partial \rho w}{\partial z}$$

En ellas p significa la presión, ρ es la densidad, f es la componente vertical del parámetro de Coriolis, u, v y w son las componentes de la velocidad y τ_{zx} y τ_{zy} se refieren a las componentes de los esfuerzos tangenciales sobre las superficies z. Las ecuaciones (1) son válidas para un océano baroclínico donde las variaciones del tiempo y las aceleraciones del campo sean pequeñas comparadas con los términos aquí considerados.

Integrando las dos primeras ecuaciones desde la superficie del mar hasta una profundidad donde se suponga que las componentes de los esfuerzos se desvanecen y efectuando la operación rotacional, tenemos:

Here p denotes pressure, ρ is density, f is the vertical component of the Coriolis' parameter, u, v and w are the velocity components, and τ_{ZX} and τ_{ZY} refer to the tangential stress components on the z-surfaces. Equations (1) are valid for a baroclinic ocean in which the time variations and field accelerations are small compared to the terms considered here.

Integrating the first two equations from the sea surface to a depth where the stress components are supposed to vanish, and performing the curl operation, gives

$$-f\ \mathrm{div}_h\ \mathbf{M} - \beta M_y + \mathrm{curl}_z \vec{\tau}_{zo} = 0 \qquad (2)$$

donde $\beta = \frac{\partial f}{\partial y}$, $\vec{\tau}_{zo}$ se refiere al esfuerzo del viento en la superficie del mar y donde

where $\beta = \frac{\partial f}{\partial y}$, $\vec{\tau}_{zo}$ refers to the wind stress at the sea surface and where

$$M_Y = \int_{-d}^{0} \rho v dz,\ M_X = \int_{-d}^{0} \rho u dz,\ \mathrm{div}_h\ \mathbf{M} = \frac{\partial M_X}{\partial x} + \frac{\partial M_Y}{\partial y}$$

son las componentes horizontales del transporte de masa (Sverdrup, 1946). La ecuación (2) es muy similar a la bien conocida de Sverdrup (1947), excepto que contiene el término adicional que comprende la divergencia horizontal del transporte de masa.

En el límite septentrional que es la costa sur de México, el transporte meridional de masas debe desvanecerse y la divergencia del transporte de masa es proporcional al rotacional del esfuerzo del viento. La divergencia del transporte de masa puede exceder en algún lugar al rotacional del esfuerzo del viento ya que el movimiento es generalmente hacia el sur y el término que contiene β, la vorticidad planetaria, se vuelve positivo.

Puede estimarse la divergencia horizontal del transporte de masa despejando $\mathrm{div}_h\ \mathbf{M}$ en la ecuación (2) y suponiendo que $\beta = 2.2 \cdot 10^{-13}$ cm^{-1} seg^{-1}; f^{-1} = $2.5 \cdot 10^4$ seg y Tendremos finalmente:

un rotacional medio $\vec{\tau}_{zo} = 5 \cdot 10^{-7}$ dinas cm^{-3} (ver Fig. 3).

are the horizontal mass transport components (Sverdrup, 1946). Equation (2) is very similar to that of Sverdrup, (1947) except that it contains the additional term involving the horizontal mass transport divergence.

At the northern boundary, which is the southern coast of Mexico, the meridional mass transport must vanish, and the mass transport divergence is proportional to the curl of the wind stress. Elsewhere the mass transport divergence is likely to exceed the curl of the wind stress, since the motion is generally to the southward, and the term containing β, the planetary vorticity, becomes positive.

An estimate of the horizontal mass transport divergence can be made by solving equation (2) for $\mathrm{div}_h\ \mathbf{M}$ and by assuming $\beta = 2.2 \cdot 10^{-13}$ cm^{-1} sec^{-1}, f^{-1} = $2.5 \cdot 10^4$ sec and an average curl $\vec{\tau}_{zo} = 5 \cdot 10^{-7}$ dynes cm^{-3} (see Fig. 3). As a result we get:

$$\mathrm{div}_h\ \mathbf{M} = -5.5 \cdot 10^{-9}\ M_y + 1.25 \cdot 10^{-2} \qquad (3)$$

donde M_y (g cm^{-1} seg^{-}) es el transporte de masa hacia el sur. Aun cuando M_y no se conoce exactamente, puede demostrarse que la contribución del término que incluye M_y hacia la divergencia del transporte horizontal de masa es pequeña, comparada con el término que contiene el rotacional del esfuerzo del viento. Para apreciar esto supongamos una velocidad arbitraria de la corriente hacia el sur de 50 cm seg^{-1}, uniforme desde la superficie del mar hasta una profundidad de 100 m. Entonces, $M_y = 5 \cdot 10^5$ g cm^{-1} sec^{-1} y $\mathrm{div}_h \mathbf{M} = 2.75 \cdot 10^{-3} + 1.25 \cdot 10^{-2}$. El primer término de la derecha es un orden de magnitud más pequeño que el segundo y puede despreciarse en primera aproximación. Así, el valor medio de la divergencia del transporte de masa es de unos $1.25 \cdot 10^{-2}$ g cm^{-2} seg^{-1}, o 1000 g cm^{-2} día^{-1}. El valor máximo es aproximadamente el doble de esta cantidad (Fig. 3).

La velocidad vertical puede estimarse integrando la ecuación de continuidad y haciendo notar que la velocidad vertical en la superficie del mar es cero. Tenemos

where M_y (g cm^{-1} sec^{-1}) is the southward mass transport. Although M_y is not accurately known, it can be demonstrated that the contribution of the term involving M_y toward the horizontal mass transport divergence is small compared to the term containing the curl of the wind stress. To see this, assume an arbitrary southward current speed of 50 cm sec^{-1} uniform from the sea surface to a depth of 100 m. Then $M_y = 5 \cdot 10^5$ g cm^{-1} sec^{-1} and $\mathrm{div}_h \mathbf{M} = 2.75 \cdot 10^{-3} + 1.25 \cdot 10^{-2}$; the first term on the right hand side is thus an order of magnitude smaller than the second and can be neglected to a first approximation. Thus the average value of the mass transport divergence is about $1.25 \cdot 10^{-2}$ g cm^{-2} sec^{-1} or 1 000 g cm^{-2} day^{-1}. The maximum value is about twice as large (Fig. 3).

The vertical velocity can be estimated from an integration of the equation of continuity, noting that the vertical velocity at the sea surface is zero. We have

$$(\rho w)_z = \mathrm{div}_h \mathbf{M} \approx f^{-1} \mathrm{curl}_z \vec{\tau}_{zo} \tag{4}$$

donde el signo $\approx$ indica igualdad aproximada. Una ecuación similar a la (4) ha sido desarrollada por Yoshida y Mao (1957). Súponiendo que $\mathrm{div}_h \mathbf{M} = 1000$ g cm^{-2} día^{-1} y que $\rho = 1$ g cm^{-3}, tenemos para la velocidad media de la surgencia durante un "*Tehuantepequero*" 10 m día^{-1}.

where the sign $\approx$ indicates approximate equality. An equation similar to (4) has been derived by Yoshida and Mao (1957). Assuming $\mathrm{div}_h \mathbf{M} = 1000$ g cm^{-2} day^{-1} and $\rho = 1$ g cm^{-3} we get for the mean upwelling speed during a *Tehuantepecer* 10 m day^{-1}.

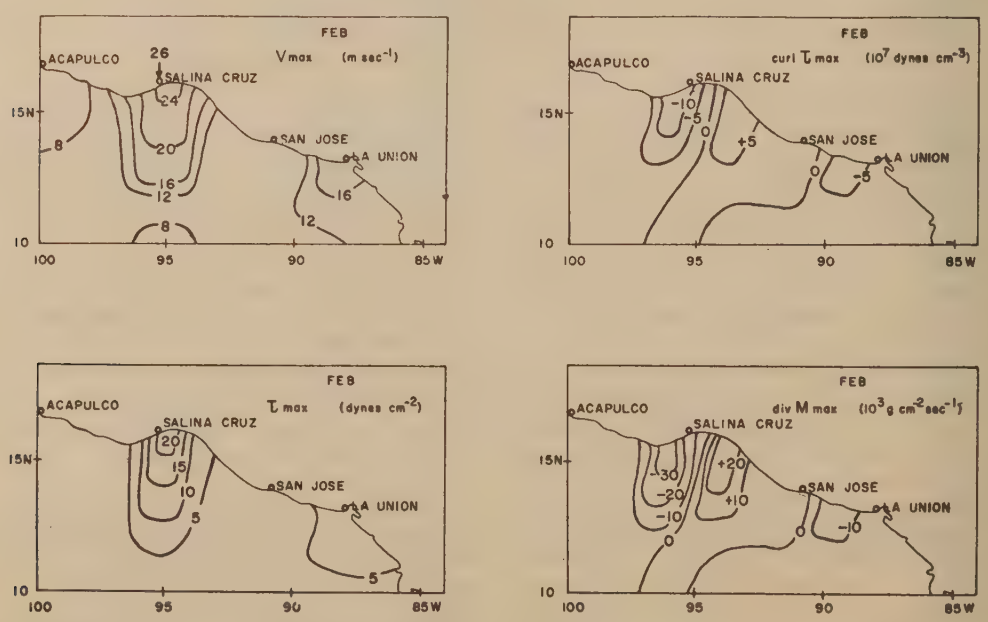


Fig. 3. Divergencia de la velocidad media máxima del viento, del esfuerzo rotacional del viento y del transporte de masa para los meses de Febrero.

Fig. 3. Mean maximum wind speed, wind stress curl and mass transport divergence for the months of February.

Un ejemplo típico de la velocidad máxima del viento en el Golfo de Tehuantepec se muestra en la Fig. 3, para el mes de Febrero. Aun cuando los valores se refieren a la velocidad escalar también representan la componente norte del viento porque su dirección durante una galerna de invierno se desvía muy poco del norte. A partir del viento se calcularon los valores de los esfuerzos y su efecto rotacional, así como de la divergencia del transporte de masa. Se observa que hacia el este de la región de grandes velocidades del viento existe una área de divergencia positiva con valores máximos de unos 0.02 g cm^{-2} seg^{-1}. Esto corresponde a una velocidad de surgencia de 17 m $día^{-1}$ aproximadamente, en el caso máximo. Ya que la divergencia positiva está asociada con movimientos hacia arriba y la divergencia negativa con movimientos hacia abajo, las temperaturas de la superficie del mar deben ser bajas en la primera área y altas en la segunda. De modo similar, el termoclinal en el área de divergencia positiva debería ser menos profundo que en el área de divergencia negativa. Las observaciones (Blackburn, MS) lo indican casi así.

La dificultad principal que encontramos con el modelo ya descrito es que no permite calcular el tiempo de reacción entre el viento y la circulación superficial. Si se agregan a las ecuaciones (1) las derivadas locales con respecto al tiempo y se llevan a cabo las operaciones efectuadas previamente, se obtiene el siguiente resultado:

A typical example of the maximum wind speed in the Gulf of Tehuantepec is shown in Fig. 3 for the month of February. Although the values refer to the scalar speed, they also represent the magnitude of the northerly wind component, because the wind direction during a winter gale deviates very little from north. From the wind were computed the wind stress, the curl of the wind stress and the mass transport divergence. It is seen that to the east of the region of high wind speeds there is an area of positive divergence with maximum values of about 0.02 g cm^{-2} sec^{-1}. This corresponds to an upwelling velocity of roughly 17 m day^{-1} in the maximum case. Since positive divergence is associated with upward motion and negative divergence with downward motion, the sea surface temperatures in the former area should be low and in the latter high. Similarly the thermocline in the area of positive divergence should be shallower than in the area of negative divergence. The actual observations (Blackburn, MS) roughly indicate this pattern.

The chief difficulty with the above described model is that it does not permit one to calculate the response time between the wind and the surface circulation. If the local time derivatives are added to equations (1) and the same operations as previously carried out, the following result is obtained:

$$\frac{\partial}{\partial t}\,\mathrm{curl}_z\,\mathbf{M} = -\frac{\partial}{\partial y}\int_{-d}^{0} u\,\frac{\partial \rho}{\partial t}\,d_z + \frac{\partial}{\partial x}\int_{-d}^{0} v\,\frac{\partial \rho}{\partial t}\,d_z - \beta M_y - f\,\mathrm{div}_h\,\mathbf{M} + \mathrm{curl}_z\,\vec{\tau}_{zo} \qquad (5)$$

que contienen tanto el efecto rotacional como la divergencia del transporte de masa. Esta ecuación es difícil de manejar. Si despreciamos la divergencia y las variaciones de ρ con el tiempo e introducimos la función de corriente del transporte de masa definida por

involving the curl as well as the divergence of the mass transport. This equation is difficult to treat. If one neglects he divergence and the time variation of ρ, and introduces the mass transport stream function, defined by

$$M_x = -\frac{\partial \psi}{\partial y} \qquad M_y = \frac{\partial \psi}{\partial x}$$

se obtiene una ecuación más simple:

a simpler equation is obtained:

$$\frac{\partial}{\partial t}\,\nabla^2\psi = -\beta\,\frac{\overset{\frac{\partial \psi}{\partial x}}{\cancel{\partial x}}}{\cancel{\partial y}} + \mathrm{curl}_z\vec{\tau}_{zo} \qquad (6)$$

El tiempo de reacción de este sistema ha sido dado por Welander (1959) como:

The time response of this system is given by Welander (1959) as

$$T = \beta^{-1} L^{-1} \qquad (7)$$

donde T es el tiempo de reacción y L una longitud característica del movimiento. En el caso del Golfo de Tehuantepec, L es del orden de 300 Km y el tiempo de reacción es del orden de $1.5 \cdot 10^5$ seg o sea casi un día y medio.

where T is the time response and L a characteristic length of the motion. In case of the Gulf of Tehuantepec, L is of the order of 300 Km and the time response is in the order of $1.5 \cdot 10^5$ sec, or about a day and a half.

ANALISIS DE SERIES DEL TIEMPO DE LA TEMPERATURA SUPERFICIAL DEL MAR Y DE LOS REGISTROS DEL VIENTO

Un ejemplo típico de variaciones no estacionales de la temperatura a lo largo de la costa sur de México y América Central se muestra en la Fig. 4. La variación estacional fue eliminada tomando las diferencias entre la media men-

TIME SERIES ANALYSIS OF SEA SURFACE TEMPERATURE AND WIND RECORDS

A typical example of nonseasonal temperature variations along the southern coast of Mexico and Central America is shown in Fig. 4. The seasonal variation was eliminated by taking differences between the monthly mean and the long

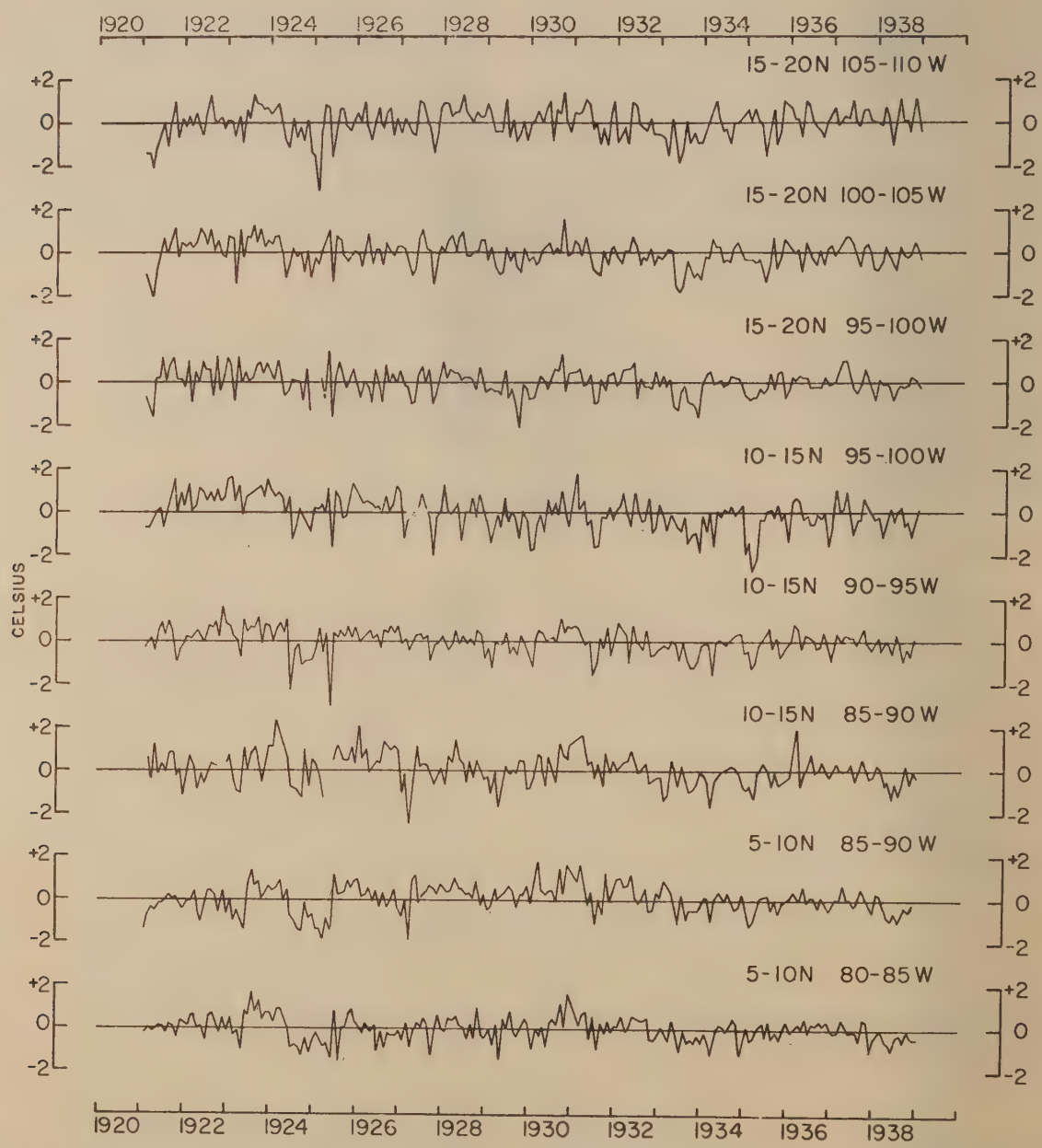


Fig. 4. Anomalías mensuales de la temperatura de la superficie del mar aguas afuera del sur de México y América Central (según Observatorio de Kobe de la Marina Imperial, 1921-1938).

Fig. 4. Monthly sea surface temperature anomalies off southern Mexico and Central America (after Imp. Marine Observatory, Kobe 1921-1938).

sual y la media de largo período para el mismo mes. Se ve que las anomalías resultantes se encuentran principalmente entre + 2° C y son de signo similar en los cuadrados de cinco grados adyacentes.

En la Fig. 5 se muestran registros de variaciones no estacionales de viento y temperatura para el área del Golfo de Tehuantepec. El intervalo de tiempo entre valores adyacentes es de diez días y cada valor representa el promedio sobre un cuadro de dos grados de latitud y longitud. Los cuadrados 14-16 N, 94-96 W y 12-14 N, 94-96 W están influenciados por fuertes galernas del norte en el invierno;

term mean for the same month. The resulting anomalies are seen to lie mostly between + 2° C and to be of similar sign in adjacent five degree squares.

More detailed records of nonseasonal temperature and wind variations are shown in Fig. 5 for the Gulf of Tehuantepec area. The time interval between adjacent values is ten days, and each value represents the average over a two degree square of latitude and longitude. The squares 14-16 N 94-96 W and 12-14 N 94-96 W are influenced by strong northerly gales in winter, the remaining two are not. Al-

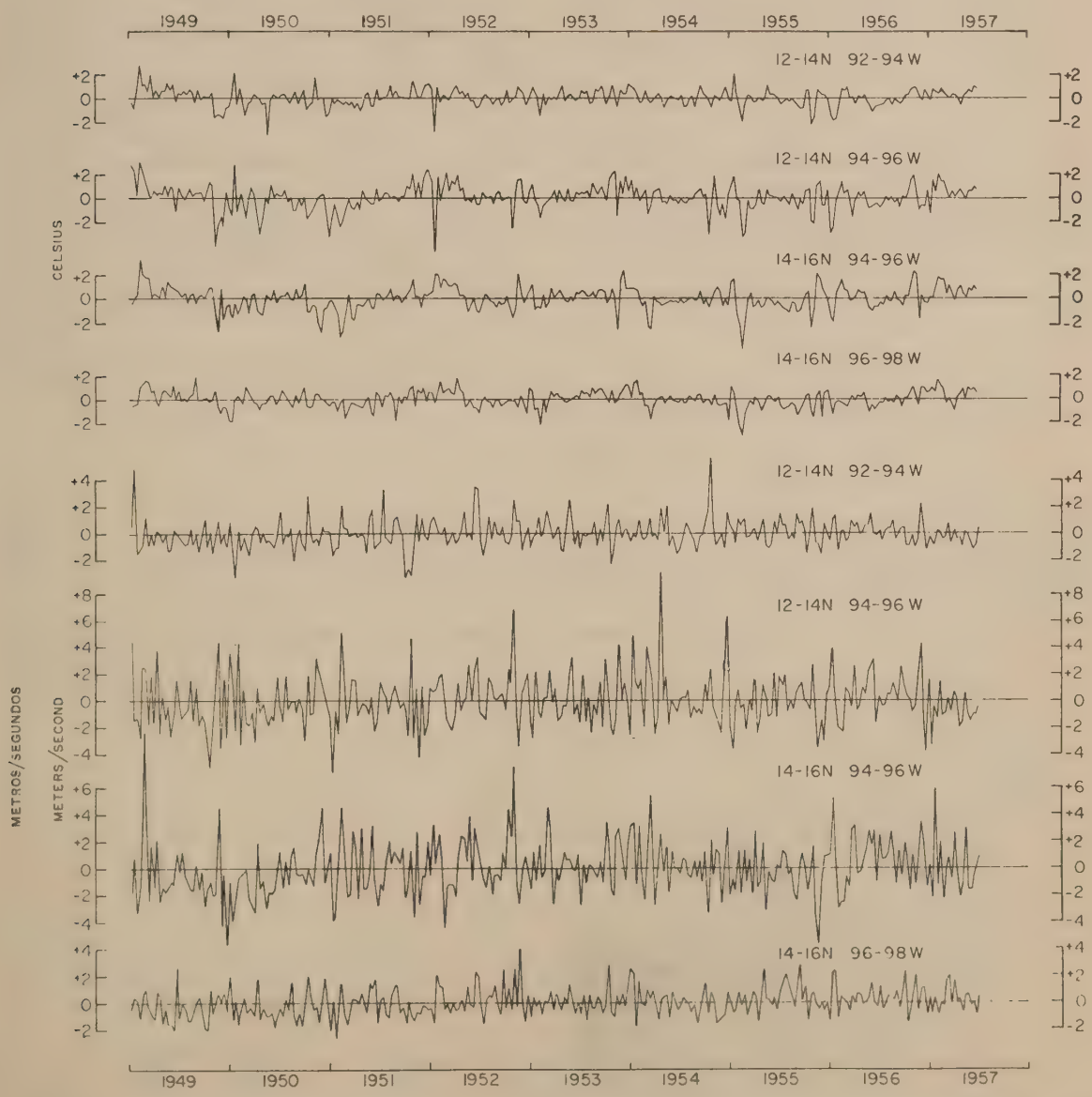


Fig. 5. Anomalías de la temperatura de la superficie del mar y de la velocidad del viento de diez días en el Golfo de Tehuantepec (según U. S. Weather Bureau, inéditas).

Fig. 5. Ten-day sea surface temperature and wind speed anomalies in the Gulf of Tehuantepec (after U. S. Weather Bureau, unpublished).

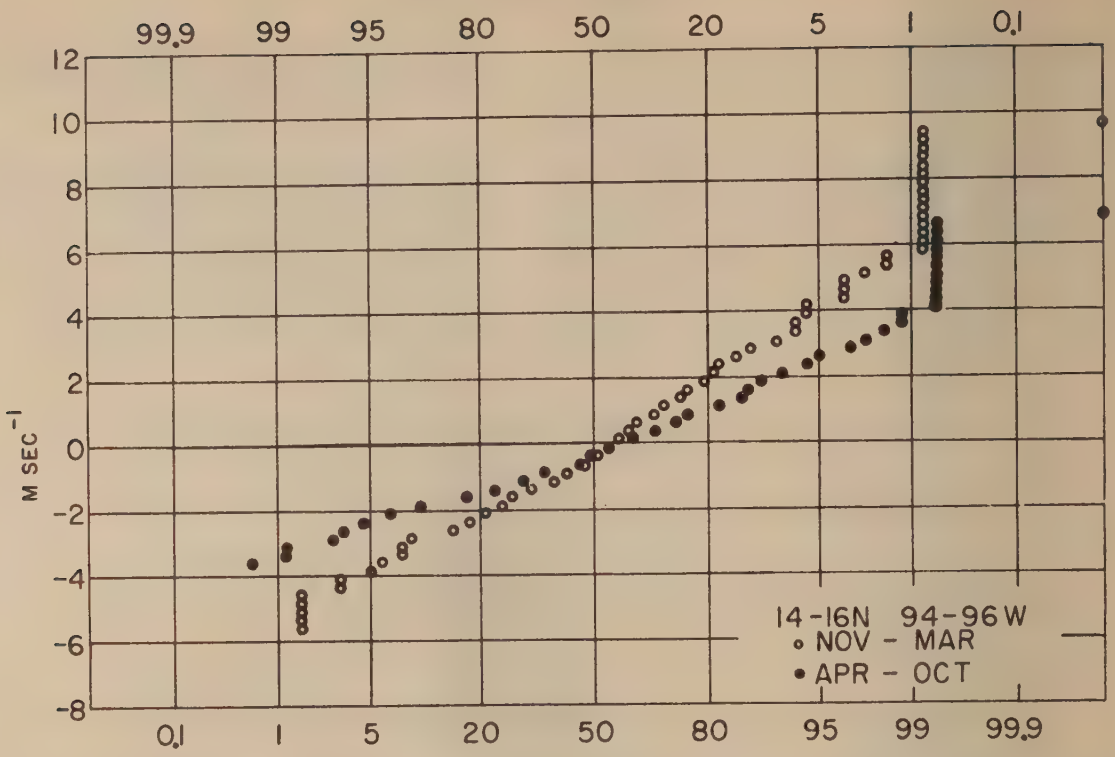
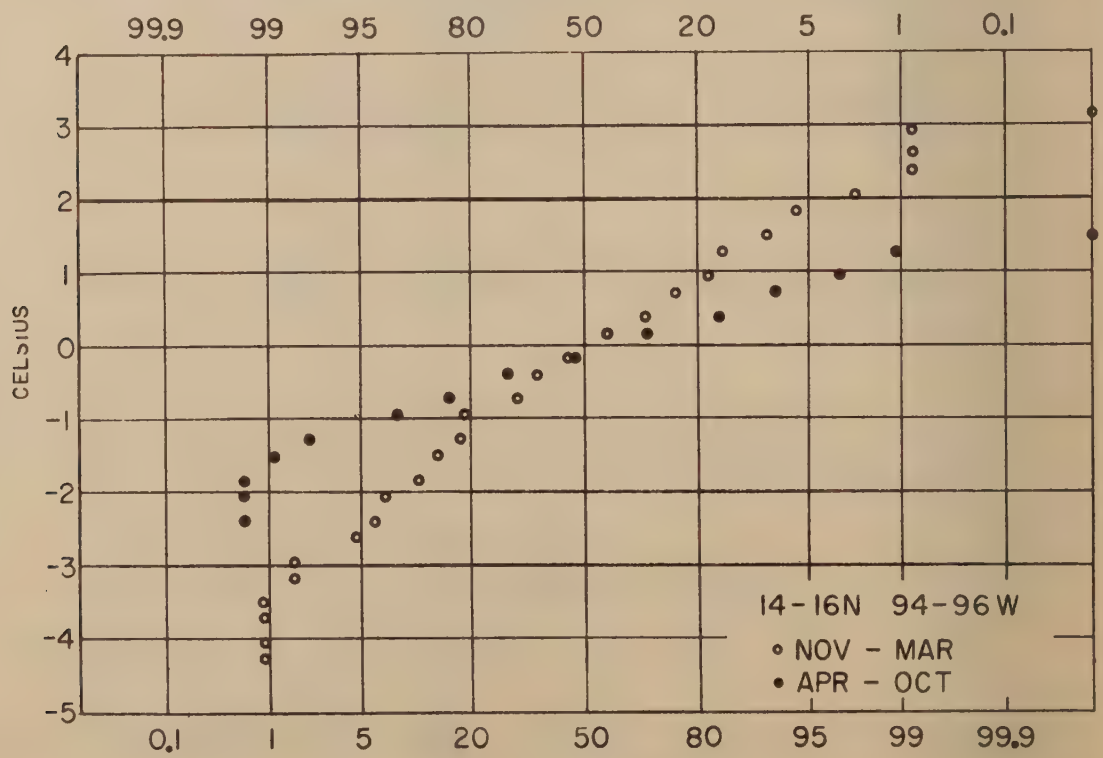


Fig. 6. Anomalías de la probabilidad de distribución de la velocidad del viento (arriba) y de la temperatura de la superficie del mar (abajo) de diez días en el Golfo de Tehuantepec.

Fig. 6. Probability distribution of ten-day wind speed (top) and sea surface temperature (bottom) anomalies in the Gulf of Tehuantepec.



los otros dos restantes no lo están. A pesar de que los detallés de esos registros varían, pueden obtenerse algunos resultados preliminares mediante su inspección visual: (1) las anomalías de las temperaturas de la superficie del mar fluctúan mucho menos que las anomalías del viento; (2) las anomalías de temperatura y del viento son mayores en los cuadrados afectados por las galernas de invierno que en los no afectados; (3) las anomalías de temperatura y del viento en cuadrados adyacentes son de signo similar; (4) parece que no hay relación significativa entre las anomalías del viento y de la temperatura. La distribución probabilística de las anomalías de temperatura y viento se muestran en la Fig. 6. Se ve que las anomalías de la temperatura están distribuidas normalmente dentro de una amplitud de $-2°$ C a $+2°$ C y que las anomalías del viento lo están dentro de una amplitud de -4 m seg^{-1} hasta $+4$ m seg^{-1}. Los extremos no están distribuidos normalmente, sino que parecen acercarse a un valor asintótico.

Para investigar hasta dónde existe una relación estadístiva significativa entre las anomalías de 10 días de la temperatura y el viento, se aplicaron métodos de análisis espectral. Los procedimientos de cómputo son los siguientes: si $\theta(t)$ y $v(t)$ se refieren a las anomalías de temperatura y de viento, entonces las funciones de correlación están dadas por

though the details of these records vary, a few preliminary results can be obtained from a visual inspection of them: (1) the sea surface temperature anomalies fluctuate much less than the wind anomalies, (2) both the temperature and wind anomalies are larger in the squares affected by the winter gales than in those not affected by them, (3) temperature and wind anomalies in adjacent squares are of similar sign, (4) there appears to be no significant relation between temperature and wind anomalies. The probability distribution of temperature and wind anomalies is shown in Fig. 6. It is seen that the temperature anomalies are normally distributed within the range of $-2°$ C and $+2°$ C and the wind anomalies within the range of -4 m sec^{-1} to $+4$ m sec^{-1}. The extremes are not normally distributed, but seem to approach an asymptotic value.

In order to investigate whether any statistically significant relation exists between the ten-day temperature and wind anomalies, methods of spectral analysis were applied. The computational procedures are as follows: Let $\theta(t)$ and $v(t)$ refer to the temperature and wind anomalies, respectively. Then the correlation functions are given by

$$\phi_{\theta\theta}(\tau) = \langle\theta(t)\theta(t+\tau)\rangle, \text{ etc.}$$
$$\phi_{\theta v}(\tau) = \langle\theta(t)v(t+\tau)\rangle \tag{8}$$

siempre que los registros sean estacionarios y $\langle\ \rangle$ denote el promedio en el tiempo sobre toda la longitud de los registros y τ se refiera al retraso en el tiempo. Las potencias de las densidades espectrales son las transformadas de Fourier de las funciones de correlación citadas y están dadas por:

provided the records are stationary and $\langle\ \rangle$ denotes the time average over the entire record length and τ refers to the time lag. The power spectral densities are the Fourier transforms of the above correlation functions and are given by:

$$E_{\theta\theta}(\omega) = \frac{2}{\pi}\int_0^\infty \phi_{\theta v}(\tau)\cos\omega\tau\, d\tau, \quad \text{etc.}$$
$$E_{\theta v}(\omega) = \frac{1}{\pi}\int_{-\infty}^{\infty} \phi_{\theta v}(\tau)\, e^{-i\omega\tau} d\tau \tag{9}$$

La coherencia entre los registros de temperatura y de viento está definida por

The coherence between temperature and wind records is defined by

$$R_{\theta v}(\omega) = \frac{E_{\theta v}(\omega)}{\left[E_{\theta\theta}(\omega)\, E_{vv}(\omega)\right]^{1/2}} \tag{10}$$

y deben encontrarse entre los valores 0 y 1. Si $R = 1$ la coherencia es perfecta; si $R = 0$ no hay coherencia. La

and must lie between the values zero and one. If $R = 1$ the coherence is perfect, if $R = 0$ there is no coherence.

fase entre las anomalías de temperatura y de viento está definida por

The phase between the temperature and wind anomalies is defined by

$$\pi_{\theta v}(\omega) = \arctan \frac{E_{v\theta}(\omega) - E_{\theta v}(\omega)}{E_{v\theta}(\omega) + E_{\theta v}(\omega)} \tag{11}$$

Si $\pi = 0$ los registros están relacionados directamente uno con otro; si $\pi = 180°$ existirá una relación inversa entre los registros.

Blackman y Tukey (1958) y Munk, Snodgrass y Tucker (1959) han dado métodos prácticos para calcular las ecuaciones (8) a (11). El análisis fue llevado a cabo en una computadora electrónica IBM 709 en el Western Data Pro-

If $\pi = 0$ the records are related directly to each other; if $\pi = 180$ degrees there exists an inverse relation between the records.

Practical methods for evaluating equations (8) to (11) are given by Blackman and Tukey (1958) and Munk, Snodgrass and Tucker (1959). The analysis was carried out on an IBM 709 electronic computer at the Western

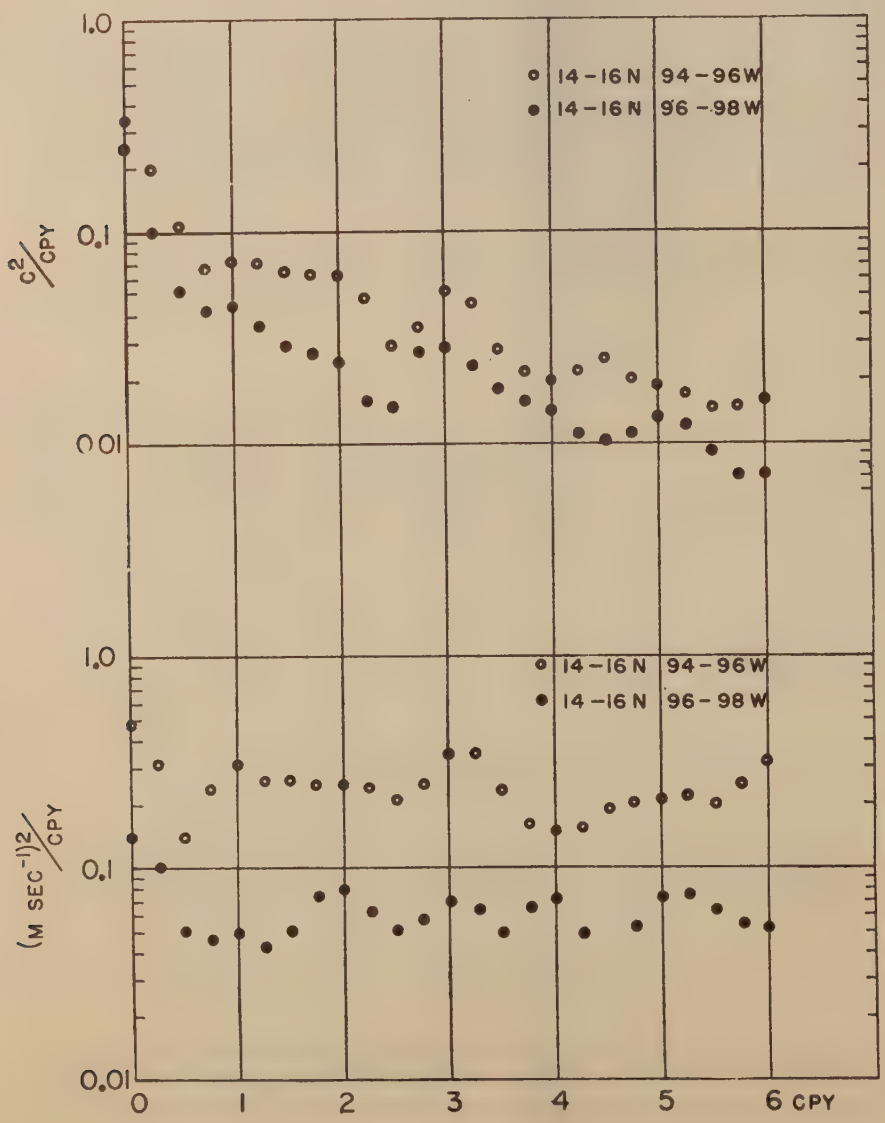


Fig. 7. Anomalías de la densidad espectral de la temperatura de la superficie del mar (izq.) y de la velocidad del viento (der.) de diez días en el Golfo de Tehuantepec.

cessing Center en Los Angeles para n = 306 observaciones y m = 24 estimaciones espectrales. Los *grados de libertad, v,* resultantes definidos por

Data Processing Center in Los Angeles for n = 306 observations and m = 24 spectral estimates. The resulting *degrees of freedom, v,* defined by

$$v = 2n/m \tag{12}$$

fueron 25.5 (Tabla 3).

was 25.5. (Table 3.)

Las densidades espectrales de las anomalías de la temperatura y el viento se ilustran en la Fig. 7. Se observa que la mayor parte está concentrada en frecuencias bajas y que no hay sino una muy pequeña contribución de parte de las frecuencias más altas. Las anomalías en los cuadrados influenciados por las galernas de invierno contienen considerablemente más fuerza que las no influenciadas por ellas. La fuerza de las anomalías del viento está concentrada más

The power spectral densities of temperature and wind anomalies are illustrated in Fig. 7. It is seen that most of the power of the temperature anomalies is concentrated at low frequencies and that there is very little contribution from higher frequencies. The anomalies in the squares influenced by the winter gales contain considerably more power than those not influenced by them. The power of the wind anomalies is concentrated rather evenly over the

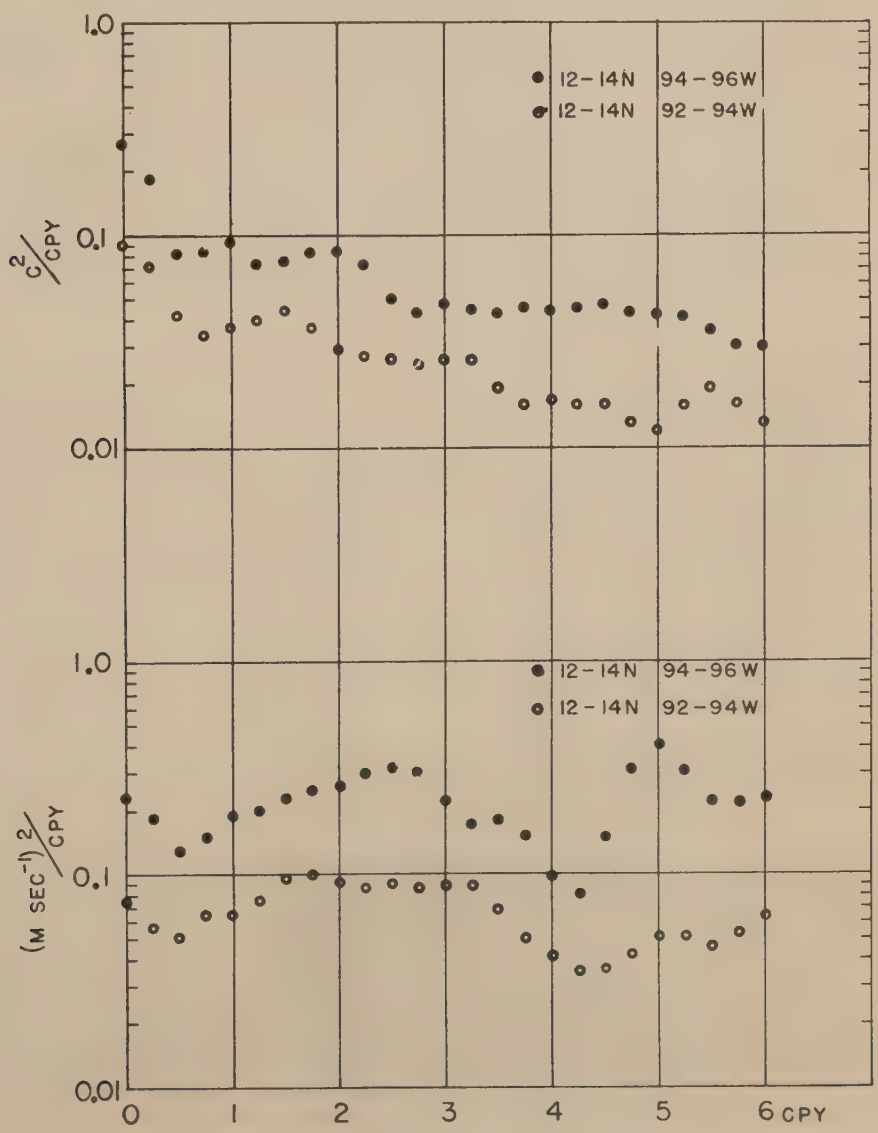


Fig. 7. Power spectral density of ten-day sea surface temperature (left) and wind speed (right) anomalies in the Gulf of Tehuantepec.

bien uniformemente sobre la gama entera de frecuencia, indicando que las componentes de alta frecuencia son tan importantes como las componentes de baja frecuencia. Debido a ello puede esperarse que las frecuencias de más de 6 ciclos por año (c.p.a.) contengan también una cantidad de fuerza considerable y que parte de esta fuerza haya contaminado el espectro del viento aquí mostrado.

La relación entre la fuerza de las anomalías de la temperatura y la fuerza de las anomalías del viento, como función de la frecuencia, se da en la Tabla 4. Se ve que la relación a bajas frecuencias es varias veces mayor que a frecuencias altas.

La coherencia por áreas entre cuadrados de dos grados adyacentes se muestra en la Fig. 8. La coherencia para anomalías de temperatura es ligeramente mejor a bajas frecuencias que a frecuencias altas, indicando que se requiere algún tiempo para que la anomalía de la temperatura se difunda a los cuadrados adyacentes. La fase de las anoma-

entire frequency range, indicating that high frequency components are as important as low frequency components. Because of this, it can be expected that frequencies beyond 6 cycles per year (c.p.y.) will also contain a considerable amount of power, and that part of this power has contaminated (aliased) the wind spectrum shown here.

The ratio of the power of the temperature anomalies to the power of wind anomalies as a function of frequency is given in table 4. It is seen that the ratio at low frequencies is several times larger than at high frequencies.

The areal coherence between adjacent two degree squares is shown in Fig. 8. The coherence for temperature anomalies appears to be slightly better at low than at high frequencies, indicating that some time is required for the temperature anomaly to spread into adjacent squares. The phase of the wind anomalies lies near zero and does not

TABLA 3

Número total de observaciones (n), número de retrasos usados (m), grados de libertad (ν), desviación standard (σ) y variación máxima (r) de la temperatura del mar (θ) y anomalías del viento (v). También se indica el 95% de límites de confianza (E) para la densidad espectral.

TABLE 3

Total number of observations (n), number of lags used (m), degrees of freedom (ν), standard deviation (σ) and extreme range (r) of sea surface temperature (θ) and wind (v) anomalies. Also shown are 95% confidence limits, (E), for the power spectra.

2° cuadrado 2° square	n	m	ν	σ_θ	σ_v	r_θ	r_v	E
	meses months	meses months		°C	m/s	°C	m/s	(°C)^2 c.p.a. o (m/s)^{2}c.p.a. c.p.y. or (m/s)^{2}c.p.y.
14-16 N 96-98 W	306	24	25.5	0.7	1.0	5.0	6.8	0.62 – 1.89
14-16 N 94-96 W	306	24	25.5	1.0	2.1	7.5	15.8	0.62 – 1.89
12-14 N 94-96 W	306	24	25.5	1.1	2.0	7.5	14.8	0.62 – 1.89
12-14 N 92-94 W	306	24	25.5	0.7	1.1	5.8	9.1	0.62 – 1.89

TABLA 4

El cociente $E_{\theta\theta}/E_{vv}$ como función de frecuencia.

TABLE 4

The ratio $E_{\theta\theta}/E_{vv}$ as a function of frequency.

Frec. Freq.	12-14N 92-94W	12-14N 94-96W	14-16N 14-16W	14-16N 14-16NW
c.p.y. c.p.a.	(°C/m sec^{-1})^2	(°C/m sec^{-1})^2	(°C/m sec^{-1})^2	(°C/m sec^{-1})^2
0	1.22	1.17	0.51	0.96
1	0.57	0.49	0.24	0.90
2	0.32	0.33	0.26	0.30
3	0.30	0.22	0.14	0.41
4	0.42	0.45	0.14	0.20
5	0.24	0.10	0.09	0.18
6	0.20	0.13	0.03	0.13

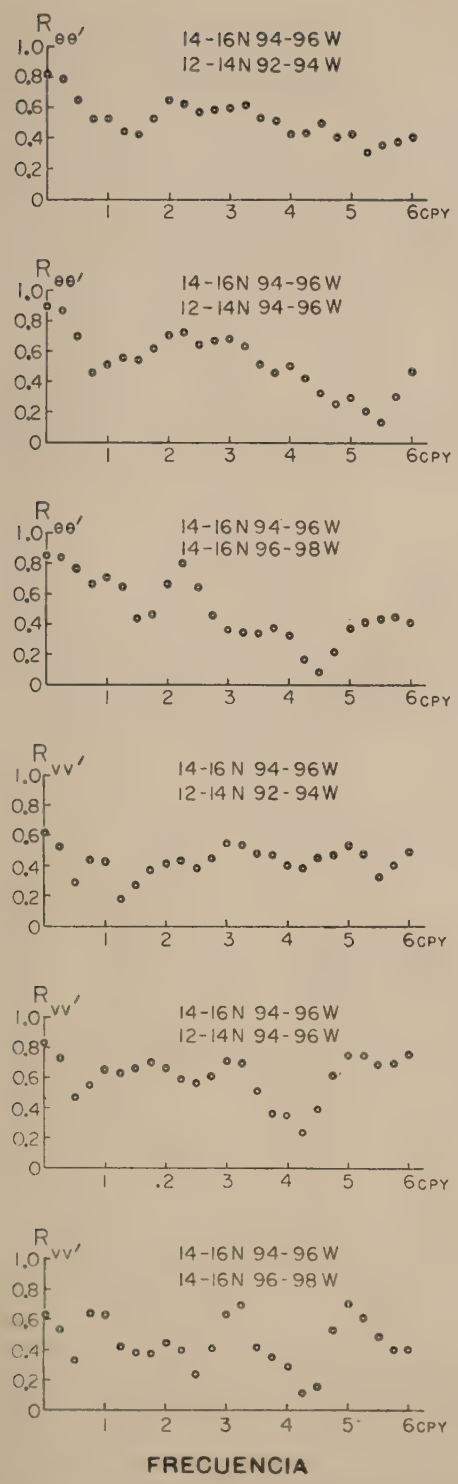


Fig. 8. Coherencia (R) y fase (π) entre anomalías en cuadrados adyacentes de dos grados. $R_{\theta\theta'}$ y $\pi_{\theta\theta'}$ referidas a las anomalías de la temperatura de la superficie del mar, Rvv' y $\pi_{vv'}$ a las anomalías de la velocidad del viento.

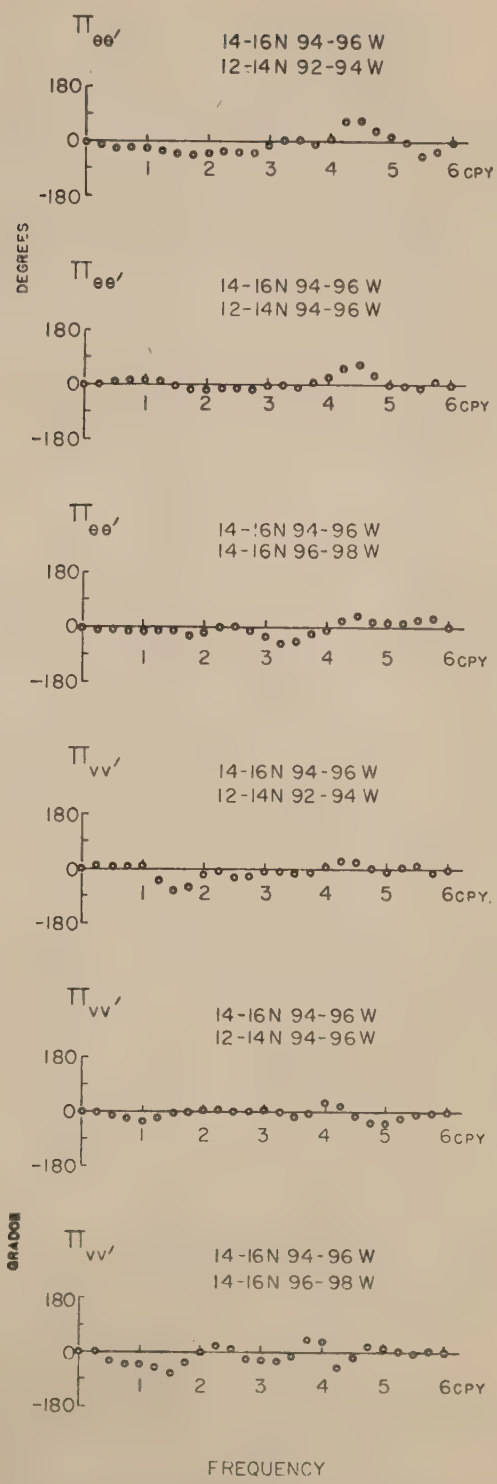


Fig. 8. Coherence (R) and phase (π) between anomalies in adjacent two degree squares. $R_{\theta\theta'}$ and $\pi_{\theta\theta'}$ refer to sea surface temperature anomalies, Rvv' and $\pi_{vv'}$ to wind speed anomalies.

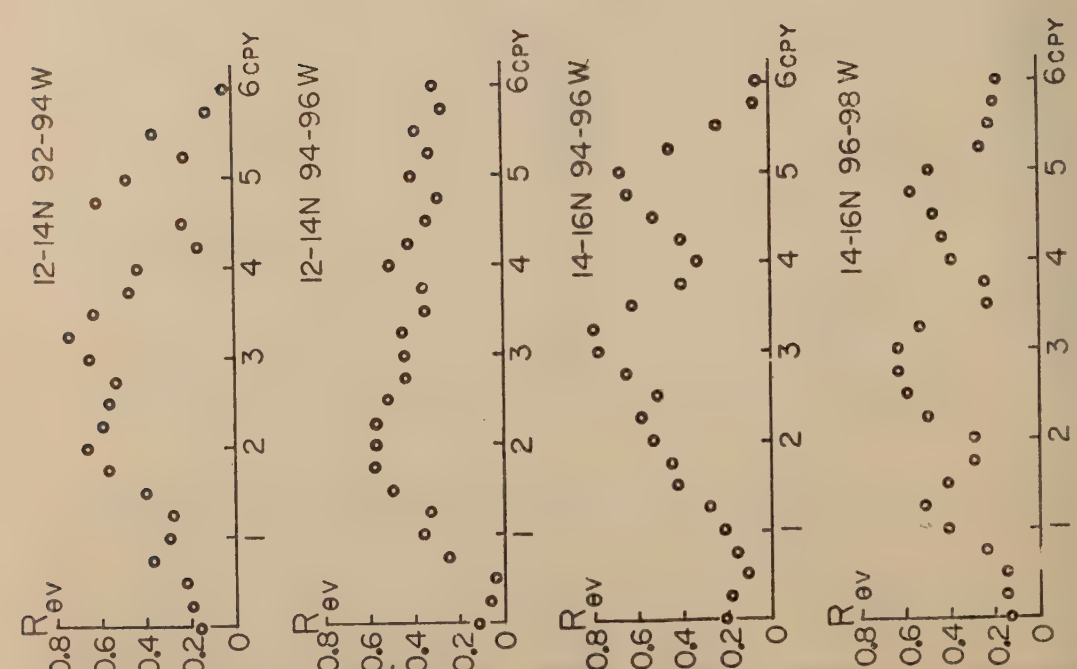


Fig. 9. Coherencia ($R_{\theta v'}$) y fase ($\pi_{\theta v'}$) entre las anomalías de la temperatura de la superficie del mar y de la velocidad del viento.

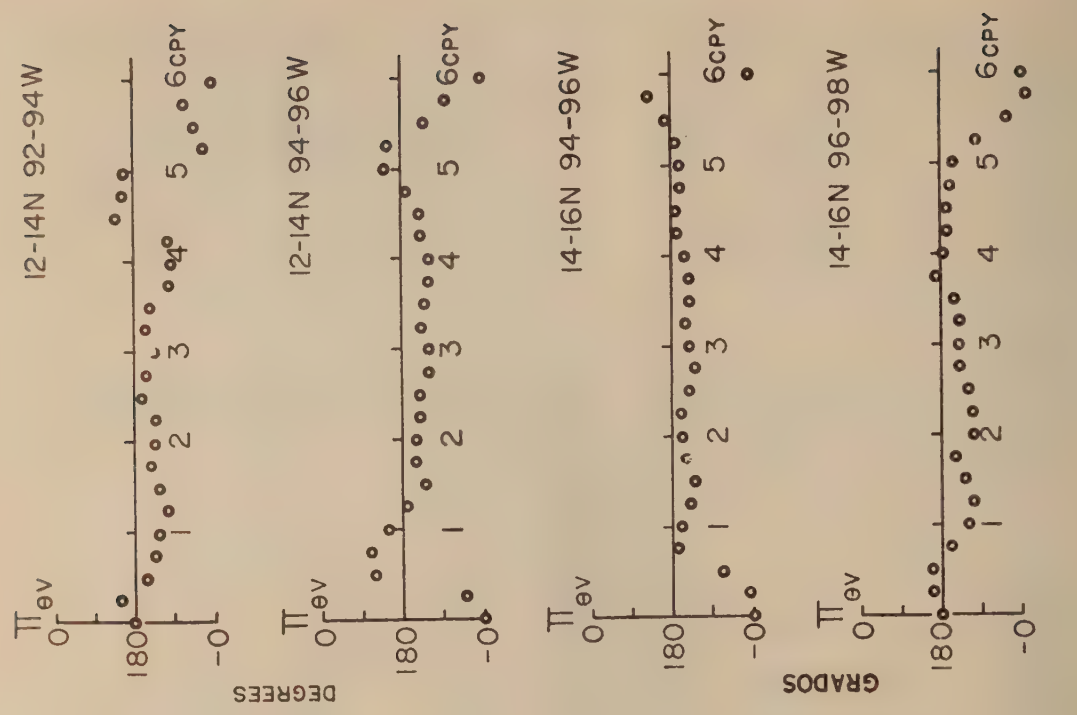


Fig. 9. Coherence ($R_{\theta v'}$) and phase ($\pi_{\theta v'}$) between sea surface temperature and wind speed anomalies.

lías del viento se encuentra cerca de cero y no depende mucho de la frecuencia, lo cual sugiere que el viento actúa simultáneamente sobre el área entera.

La coherencia y la fase entre las anomalías de temperatura y las del viento se muestra en la Fig. 9. La coherencia fluctúa ampliamente con la frecuencia y varía entre 0 y 0.8. Es baja en ambos extremos del espectro y muestra algunos máximos mal definidos alrededor de 3 c.p.a. y 5 c.p.a. La fase se dispersa alrededor de 180° para frecuencias entre 2 c.p.a. y 5 c.p.a. e indica una relación inversa entre las anomalias de la temperatura y el viento. Si se supone una coherencia media para el espectro de 0.4, no más del 16% de las anomalías están relacionadas unas con otras. Esto puede ser debido parcialmente a la imperfección de los datos, pero es más seguro que la surgencia representa un fenómeno mucho más complejo que lo que puede describirse con solamente los datos de vientos.

depend much upon frequency, which suggests that the wind acts simultaneously over the entire area.

The coherenece and phase between temperature and wind anomalies are shown in Fig. 9. The coherence fluctuates widely with frequency and varies between 0 and 0.8. It is low at both ends of the spectrum and shows some ill defined maxima around 3 c.p.y. and 5 c.p.y. The phase scatters around 180 degrees for frequencies between 2 c.p.y. and 5 c.p.y. and indicates an inverse relationship between temperature and wind anomalies. If an average coherence of 0.4 is assumed for the spectra, not more than 16% of the anomalies are related to each other. This may be partly due to the crudeness of the data, but it is more likely that upwelling represents a much more complex phenomenon than can be described by the wind data alone.

CONCLUSION

El Golfo de Tehuantepec es notable por fuertes surgencias en el invierno, las cuales llevan a temperaturas superficiales del mar varios grados más bajas que en otras partes a lo largo de la costa del sur de México. La causa primaria de la surgencia es el viento con fuerza de galerna que sopla a veces desde el norte a través del Istmo de Tehuantepec sobre el Océano Pacífico. El efecto del viento se observa a varios centenares de kilómetros hacia el sur. Se investigó la relación entre los vientos y las temperaturas desde un punto de vista dinámico y desde un punto de vista estadístico.

El tratamiento dinámico llevó al resultado de que la surgencia en el Golfo de Tehuantepec está relacionada con el rotacional de los esfuerzos del viento y que se pueden esperar durante los nortes surgencias de 10 m día^{-1}. El tratamiento estadístico mostró que hay una relación inversa pero débil entre las temperaturas de la superficie del mar tomadas cada 10 días y las anomalías del viento.

CONCLUSION

The Gulf of Tehuantepec is noted for strong upwelling in winter which leads to sea surface temperatures several degrees lower than elsewhere along the coast of southern Mexico. The primary cause of upwelling is the gale force wind blowing at times from the north across the Isthmus of Tehuantepec into the Pacific Ocean. The wind effect is felt several hundred kilometers to the southward. The relation between winds and temperatures was investigated from a dynamical point of view and a statistical point of view.

The dynamical approach led to the result that upwelling in the Gulf is related to the curl of the wind stress, and that upwelling speeds of 10 m day^{-1} can be expected during northers. The statistical approach showed that there is an inverse, but rather weak relation between ten-day sea surface temperature and wind anomalies.

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WARREN S. WOOSTER AND MALVERN GILMARTIN

THE PERU-CHILE UNDERCURRENT

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The Peru-Chile Undercurrent[1]

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ABSTRACT

The presence of a southward-moving undercurrent along the west coast of South America, underlying the Peru Current at depths of several hundred meters, has been established by direct measurements with parachute drogues, by calculations of geostrophic motion, and by analysis of the distributions of salinity and dissolved oxygen. The undercurrent extends from northern Peru to at least 41°S. Speeds of 4–10 cm/sec were measured off Peru and northern Chile; the geostrophic transport appears to decrease downstream, from 21×10^6 at 5°S to about 3×10^6 m3/sec at 15°S. At its coastal edge the flow parallels the edge of the continental shelf. South of 15°S, waters of the undercurrent are characterized by relatively high salinity and temperature as well as low oxygen content.

The surface currents which flow equatorward along the eastern margins of the major ocean basins are relatively well known. They include the California and Peru currents in the Pacific Ocean and the Canary and Benguela currents in the Atlantic Ocean. But little, if anything, is known about the

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subsurface circulation in these regions, although there are some indications of poleward coastal currents several hundred meters beneath the equatorward surface flow.

For example, a common feature of the density distribution on cross-stream profiles off such coasts is a deepening of the isopycnals shoreward below the ascending isopycnals characteristic of coastal upwelling (Wooster and Reid, in press). A similar deepening (or trough) is also found along the equator in association with the Equatorial Undercurrent or Cromwell Current (Knauss, 1960). In the coastal region geostrophic computations based on this density distribution indicate the presence of a subsurface countercurrent, or undercurrent.

The similarity in distributions of mass and circulation in the equatorial and eastern boundary coast regions has been noted by Yoshida and collaborators (Yoshida, 1955; Yoshida and Tsuchiya, 1957; Yoshida 1958, 1959), who have made a theoretical investigation of the boundary phenomena. But until now no one has actually measured a coastal undercurrent and attempted to relate such measurements to other physical and chemical observations made in the vicinity at the same time.

In a recent paper Wooster and Reid (in press) discussed the evidence for coastal undercurrents on the eastern boundary coasts of California, Peru and Chile, northwest and southwest Africa. The scarcity of data suggested the desirability of including direct current measurements in the scientific program of the STEP-I Expedition of the University of California's Scripps Institution of Oceanography. The present paper is based primarily on observations of this expedition aboard R/V Horizon off the west coast of South America during October 1960.

Observations and Methods. The track and station arrangement of the STEP-I Expedition are shown in Figs. 1 and 2. Observations along the profiles consisted of oceanographic stations at 40–100 mile intervals with numerous BT and surface salinity observations between stations. On most stations measurements were made between the surface and at least 1000 m, and in some cases to depths of several kilometers. Station measurements included temperature, salinity, dissolved oxygen, phosphate, silicate and nitrite, made by conventional methods (salinities were determined with a conductivity-type salinometer: Paquette, 1959).

South of Talara at six locations, measurements of surface and subsurface currents were made with parachute drogues close to shore (Fig. 2) but beyond the edge of the continental shelf because the undercurrent was believed to be a boundary phenomenon and because it was desired to use offshore islands as reference points for navigational control. The drogues, similar to those described by Jennings and Schwartzlose, 1960 (see Volkmann, *et al.*, 1956, for discussion of the method), consisted of seven-meter diameter aviator's

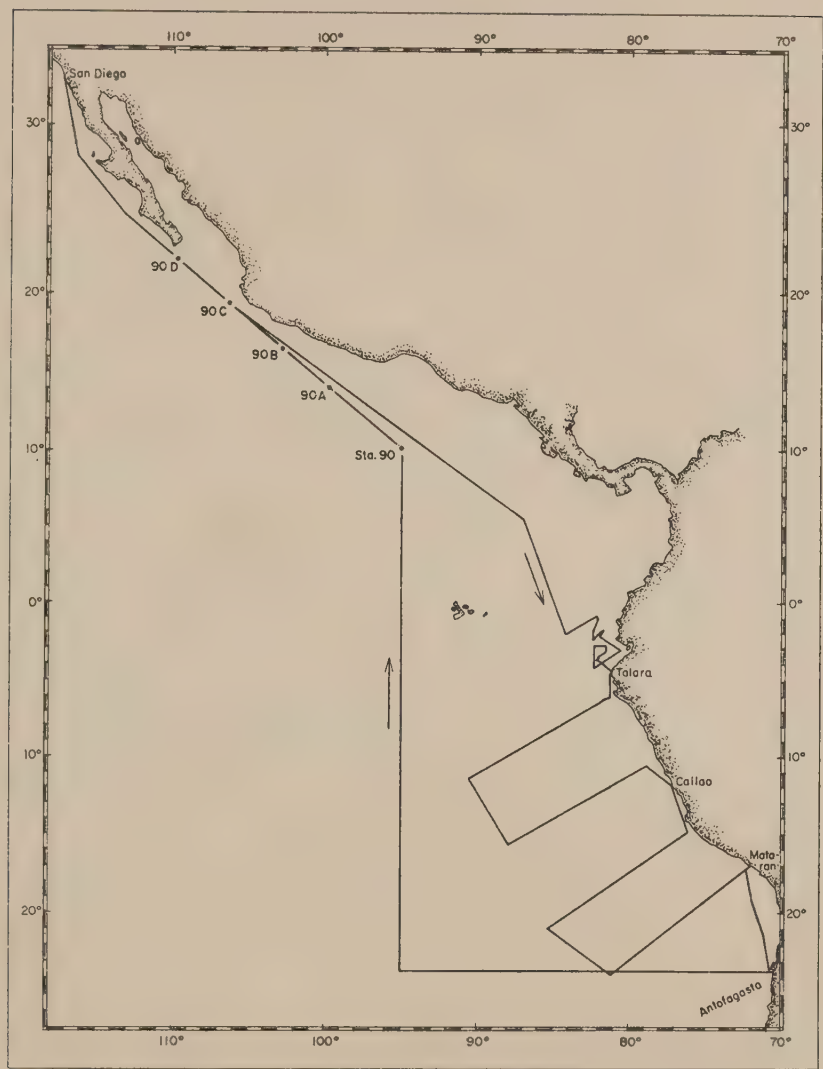

Figure 1. Track chart of STEP-I Expedition, 15 September to 14 December, 1960.

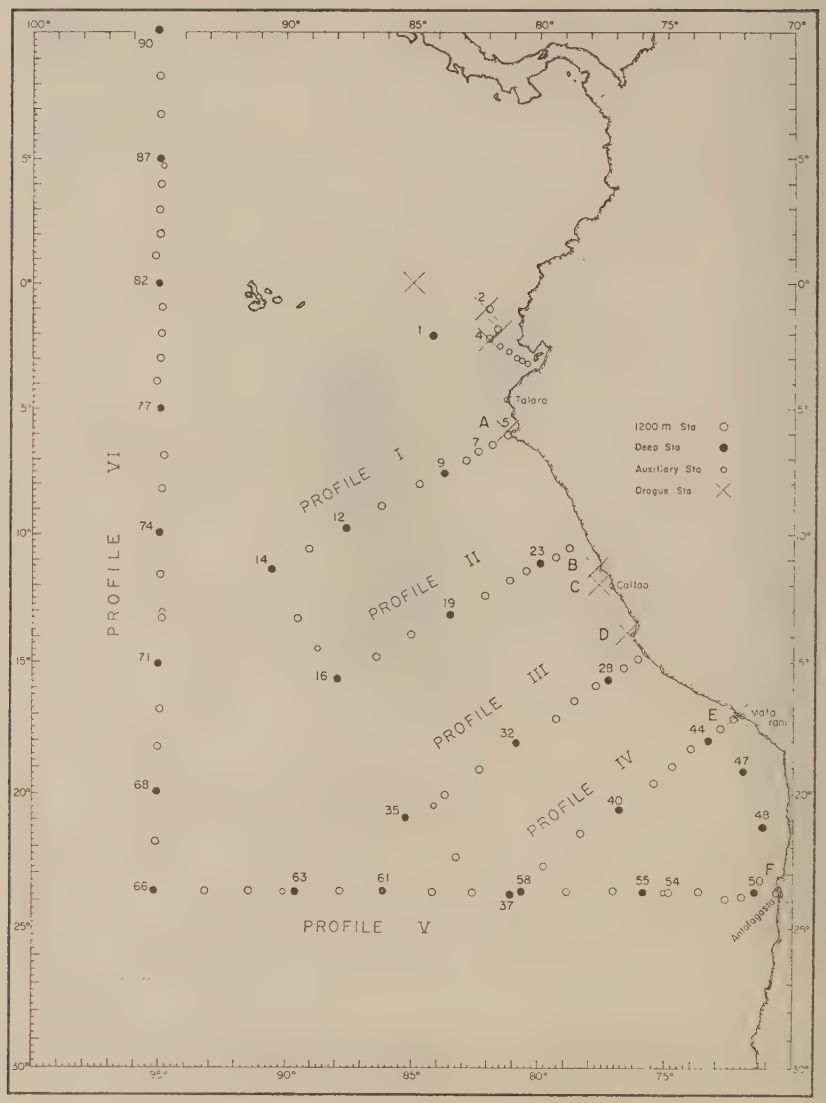

Figure 2. Station plan of STEP-I Expedition.

parachutes connected by wire to seven-meter bamboo poles suitably equipped to serve as surface indicators of the drogue positions.

At each location two drogues were customarily placed at each of the following approximate depths as indicated by the length of wire used: 10 m, 100 or 150 m, 250 or 300 m. The true depth differs only slightly from the wire length (Volkmann, *et al.*, 1956). The parachutes at 10 m were connected to the surface floats with 7×7 aircraft cable, 2.4 mm diameter; for deeper parachutes, including those of the two reference drogues, 2.1 mm diameter music wire was used; connections were made with "Nicopress" sleeves. On the southernmost station, combinations of aircraft cable and music wire were used due to shortage of the latter. Parachutes were sent unopened to the desired depth, weights at the parachute apex then being dropped by a time release device.

Along the Peruvian coast, numerous small steep islands are perched near the edge of a narrow continental shelf, and on four of the six stations, these were used as reference points for position control. On the other two stations, where such islands were not available, parachutes at 1000 m were used as reference points. After a suitable interval following launching, the positions of drogues relative to the reference point were determined with a U.S. Navy SPS-5 radar and by occasional visual inspection. Ranges and bearings were determined at approximately half-hour intervals, the total tracking time varying from 18–43 hours. It was usually possible to track all drogues on a station simultaneously, from ranges of several thousand meters (the radius of sea return) to more than 14,000 m (under ideal wind and sea conditions). After 12–24 hours, surface drogues had usually moved out of range and were abandoned so that subsurface drogues would not be lost.

In analysizing these drogue measurements, the apparent relative motion of the drogues was corrected for the effect of wind and surface current on the surface float and for drag of the connecting wire. A discussion of drag forces acting on the various components of the drogue system has been presented by Volkmann *et al.* (1956). The convenient graphical method of Brown (in press) was used for computing the necessary corrections. As a rule, corrections for forces acting on the surface float were significant whereas those for wire drag were negligible. A discussion of the errors involved in these current measurements is given in the Appendix.

Evidence from drogue measurements. Pertinent information concerning the drogue stations and a summary of measurements are presented in Table I. The observed drogue trajectories, uncorrected for drag of the wire and surface apparatus, are shown in Figs. 3–8.

Corrected mean current vectors, estimated by comparing the first and last reliable drogue positions, are shown superposed on charts of bottom topography in Fig. 9.

TABLE I. SUMMARY OF DROGUE MEASUREMENTS.

Drogue Station	Station Depth (m)	Width of Cont. Shelf (km)	Distance Offshore (km)	Mean Wind cm/sec dir °T	Depth of drogue (m)	No. of drogues	Max. Time Observed (hours)	Observed Drift speed cm/sec	Observed Drift direction °T	Corrected Drift speed cm/sec	Corrected Drift direction °T
A	320	7	26	53/170	10	3	12.5	11.9 ± 3.5	292 ± 3	11	287
					150	2	28.1	3.1 ± 1.6	162 ± 15	5	160
					300	2	34.8	6.4 ± 1.3	151 ± 18	7	152
B	300	35	49	30/162	10	2	20.4	25.8 ± 0.9	272 ± 2	26	270
					100	2	35.2	9.8 ± 0.6	239 ± 4	8	225
					250	2	35.2	9.3 ± 1.8	199 ± 5	9	192
C	290	65	73	76/152	10	2	5.2	29.3 ± 2.3	306 ± 5	28	314
					100	2	18.1	9.5 ± 1.0	312 ± 8	5	310
					250	2	18.1	8.9 ± 0.7	318 ± 9	5	321
D	465	11	34	53/156	10	2	19.6	18.1 ± 0.4	352 ± 3	17	353
					100	2	6.2	2.6 ± 1.2	344 ± 38	0	–
					250	2	19.6	1.7 ± 1.0	321 ± 76	1	202
E	650	4	10	2/123	10	4	15.5	28.7 ± 3.2	308 ± 7	29	308
					100	2	34.0	17.5 ± 0.7	327 ± 2	15	331
					250	2	33.0	3.9 ± 1.8	141 ± 12	7	133
F	3135	3	27	37/168	10	2	22.7	19.3 ± 0.5	065 ± 2	19	067
					100	2	33.2	3.1 ± 0.3	151 ± 16	4	179
					250	2	33.2	4.8 ± 0.2	202 ± 5	6	211

A – 6 Oct. 1960, 5°57′S, 81°26′W; B – 19 Oct. 1960, 11°26′, 78°05′W; C – 25 Oct. 1960, 11°58′S, 77°49′W; D – 27 Oct, 1960, 13°51′S, 76°43′W; E – 7 Nov. 1960, 17°0′S, 72°15′W; F – 12 Nov. 1960, 23°31′S, 70°53′ W.

Figure 3. Uncorrected drogue trajectories, St. A (5°57′S, 81°26′W). Surface drogues indicated by dash-dot lines, intermediate drogues by dashed lines, and deep drogues by solid lines. Ticks along trajectory indicate 2-hour time intervals.

Figure 4. Uncorrected drogue trajectories, St. B (11°26′S, 78°05′W); symbols as in Fig. 3.

Figure 5. Uncorrected drogue trajectories, St. C (11°58′S, 77°49′W); symbols as in Fig. 3.

Within the time periods during which drogues were tracked, fluctuations in speed and direction are evident and are undoubtedly related to the forces causing and modifying the flow (such as wind stress and tides); these will not be examined in detail here. However, the good coherence between drogues at the same depths (Figs. 3–8) suggests that the observed motion is a reliable indication of water movement.

Surface Motion. Fifteen drogues were placed at a depth of 10 m on the six stations. In all cases they moved rapidly out of the operational area and thus were followed for relatively short periods (5–23 hours). On all but the southernmost station, surface drift was toward the northwest (270°–353°), with mean speeds of 11–29 cm/sec. This motion is consistent with the generally accepted picture of surface flow in the Peru Current.

On the southernmost station, average surface drift was toward 067° at a speed of 19 cm/sec; during the first eight hours motion was toward the east, but as the drogues approached the coast they swung toward the northeast and speeded up. Offshore the eastward motion (090° ± 4°) was at a speed of 16–17 cm/sec. Five days later, at a position 35 km west of the drogue station,

Figure 6. Uncorrected drogue trajectories, St. D (13°51′S, 76°43′W); symbols as in Fig. 3.

a surface current measurement by geomagnetic electrokinetograph[3] gave a velocity of 13 cm/sec toward 097°, consistent with the observed motion of the surface drogues.

Subsurface Motion. In most cases subsurface movement was significantly different from that at the surface. At four stations, the deepest drogues moved

3 On the other stations such measurements were not possible because of the proximity of the magnetic equator.

Figure 7. Uncorrected drogue trajectories, St. E (17°00′S, 72°15′W); symbols as in Fig. 3.

southward (133°–211°) at speeds of 5–9 cm/sec; on a fifth station (13°51′S), corrected motion was also southward but at almost negligible speed (1 cm/sec); and on the sixth (11°58′S), motion was toward the northwest. On three stations, the drogues moved southward (160°–225°) at 4–8 cm/sec at intermediate depths and faster at greater depths, suggesting that the principal motion lies somewhat deeper than 100–150 m.

Thus on all but one station there was some indication of a subsurface current flowing southward along the coast in a direction more or less opposite to that of the surface flow. The anomalous station (11°58′S), with motion

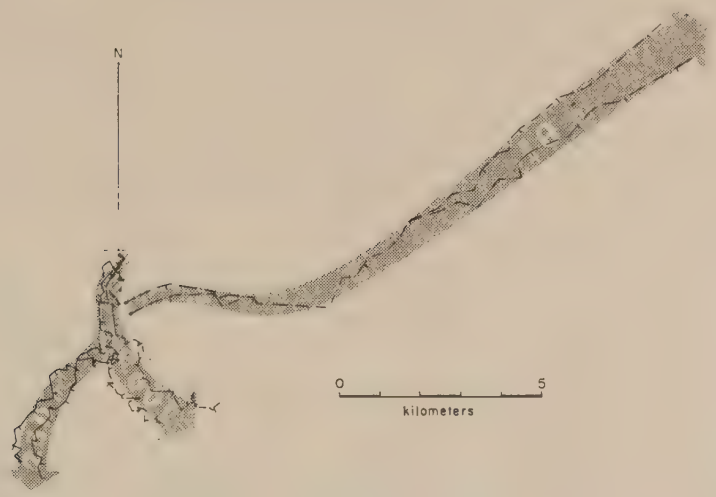

Figure 8. Uncorrected drogue trajectories, St. F (23°31′S, 70°53′W); symbols as in Fig. 3.

at all levels toward the northwest, was the shallowest one occupied, and was located off a wider continental shelf than were the other stations.

The direction of subsurface motion is closely related to the direction of the 100 fm contour (Fig. 9). This relationship is particularly striking on the stations at 17° and 23°30′S, between which there occurs a major change in orientation of the edge of the continental shelf.

Evidence from Distribution of Properties. A southward current below the surface along the west coast of South America has been discussed by Gunther (1936), whose principal evidence for this circulation is a meridional profile of salinity about 100 miles offshore, extending from 2°–35°S (his fig. 42). The high salinity tongue reaching southward from about 15°S is considered indicative of a coastal return current which deepens as it flows southward – from about 100 m at 15° to 300 m at 35°S. Other characteristics of this water are said to be relatively high temperature and low oxygen content.

A profile analogous to that of Gunther has been constructed (Fig. 10), as far south as 24° from STEP-I data, and to 41°S from Chiper and Ob Cruise 3 data (manuscript data from U.S. Hydrographic Office and World Data Center A, respectively). Evident here also are the high salinity tongue reaching south from 15° to at least 41°S between low salinity waters of southern origin and a downstream decrease from greater than 34.8‰ at 15°S to less than about 34.5‰ at 41°S. At the same time thermosteric anomaly at the core of the tongue decreases, from 160 to less than 140 cl/T (centiliters per

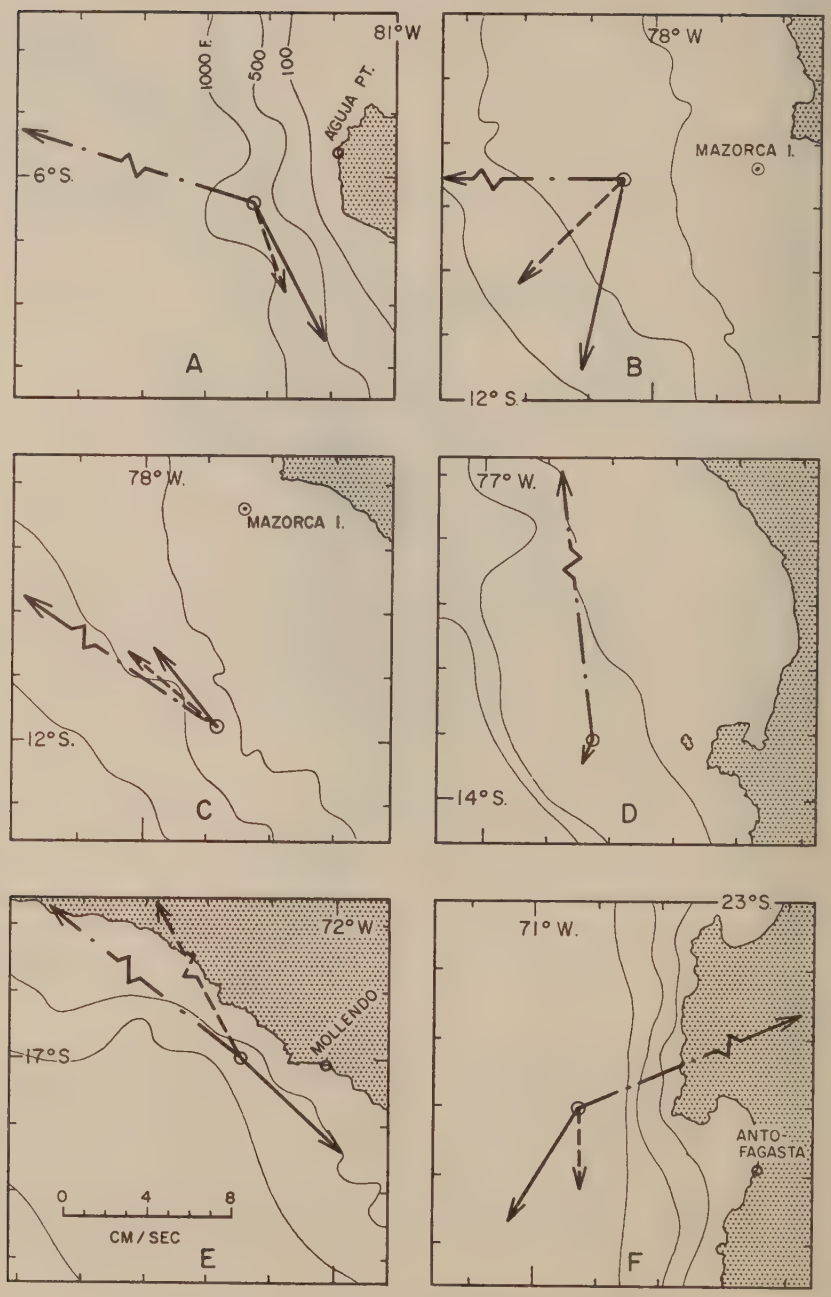

Figure 9. Corrected mean current vectors and bottom topography. Surface drogue vectors (not to scale) indicated by dash-dot lines, intermediate vectors by dashed lines, and deep vectors by solid lines.

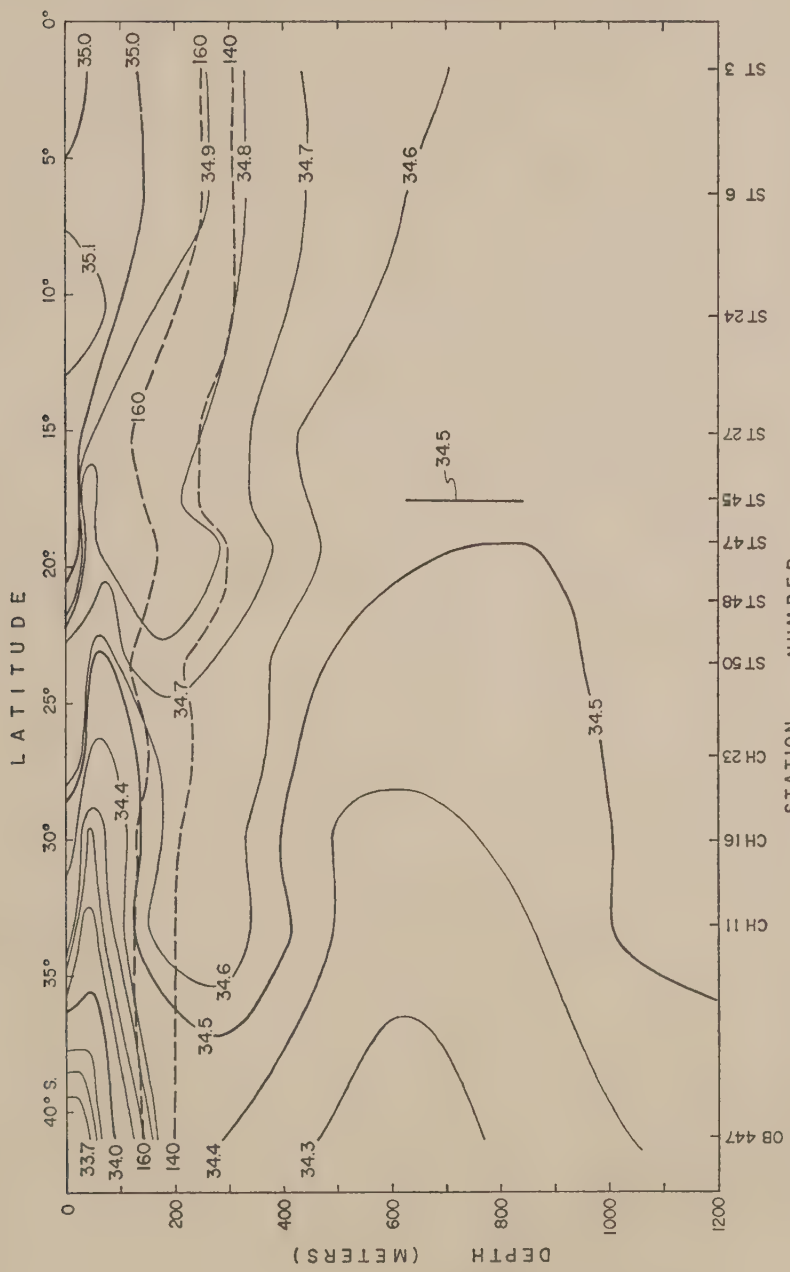

Figure 10. Distribution of salinity (‰) on a profile parallel to the west coast of South America about 100 miles offshore. Stations from STEP-I, CHIPER, and OB' Cruises (see text). Isanosteres of 140 and 160 cl/T shown by dashed lines.

ton), suggesting that attenuation of the tongue is due to mixing with water of lower temperature.

A profile of dissolved oxygen from the same data sources (Fig. 11) shows clearly the low oxygen content of the southward-moving water in contrast to the much higher values in the underlying water. Off the Peruvian coast subsurface water contains about 0.1 ml/L of dissolved oxygen; as the water moves southward, mixing with deeper water causes the oxygen content in the minimum layer to increase to about 1.7 ml/L at 41°S. Highest values of salinity and lowest values of dissolved oxygen are observed next to the coast (Figs. 12 and 13) with attenuation of the maximum and minimum offshore. Width of the high-salinity, low-oxygen tongue decreases downstream. At the southern end of the profile the undercurrent is also evidenced by phosphate and silicate maxima (see Ob' St. 447 data).

Evidence of an undercurrent can also be seen in the profiles of geostrophic velocity based on STEP-I data. In making the computations, thermosteric anomaly was used rather than specific volume anomaly, this approximation being considered adequate for the purposes of this paper (Montgomery and Wooster, 1954). A reference level of 1000 db was used; although motion on this surface is not known, it is probably small relative to that of the overlying water.[4] The use of a conductivity bridge to determine salinity reduces the effect of measurement errors on geopotential anomaly to less than 0.01 dyn m (Wooster and Taft, 1958), and reporting relative geostrophic speeds to the nearest few cm/sec may be justified.

Geostrophic speeds perpendicular to the five profiles extending offshore are shown in Figs. 14–18. Speeds less than 2 cm/sec have been considered negligible. Some southward motion is apparent in each of the profiles; it predominates in the northernmost profile and becomes progressively less intense to the south. Highest southward speeds, shown in the coastal portions of the profiles, usually appear at depths of 100–200 m. In Profiles II and III, the principal southward flow seems to separate from the coast, although some southward motion is still apparent between coastal station pairs as far south as Profile IV. On Profiles IV and V, southward geostrophic flow is very much reduced. Speeds decrease from 20 cm/sec in the northernmost profile to about 2 cm/sec on Profile IV. Southward transport decreases from about 21×10^6 on Profile I to about 3×10^6 m^3/sec on Profile III.

Discussion. Results from the parachute drogue measurements and from analyses of the distribution of properties and the geostrophic computations demonstrate clearly the presence of a southward undercurrent along the coast of Peru and Chile. Characteristics of the undercurrent can be summarized as follows:

4 In one instance (see Appendix) the motion of a 1000 m reference drogue was estimated to be 1 cm/sec or less.

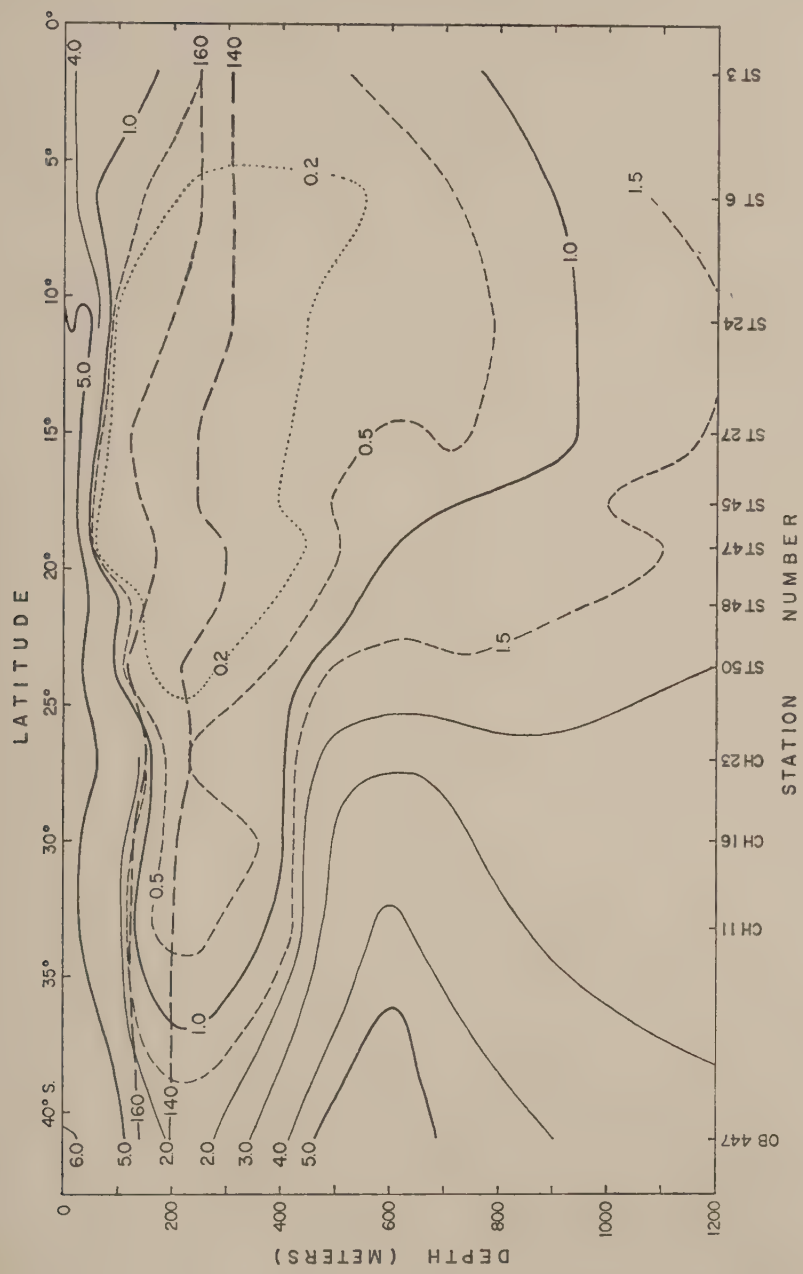

Figure 11. Distribution of dissolved oxygen (ml/L) on same profile as Fig. 10.

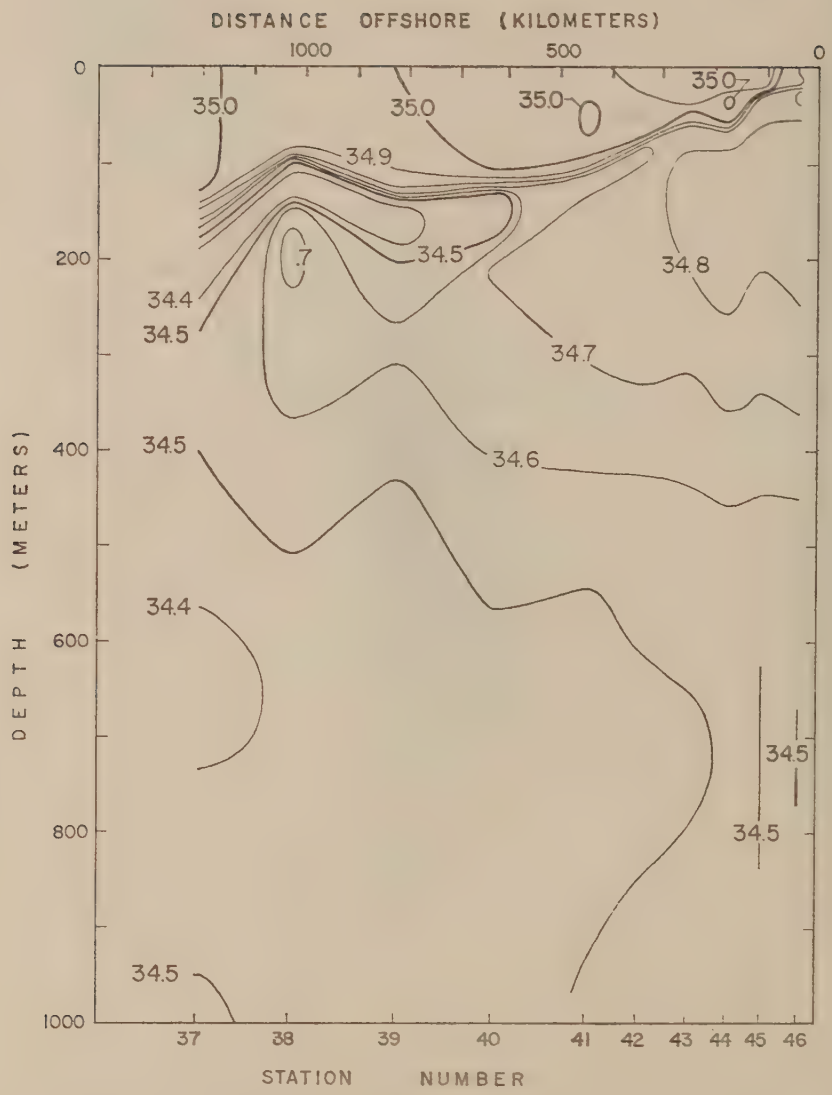

Figure 12. Distribution of salinity (‰) on Profile IV; see Fig. 2 for location.

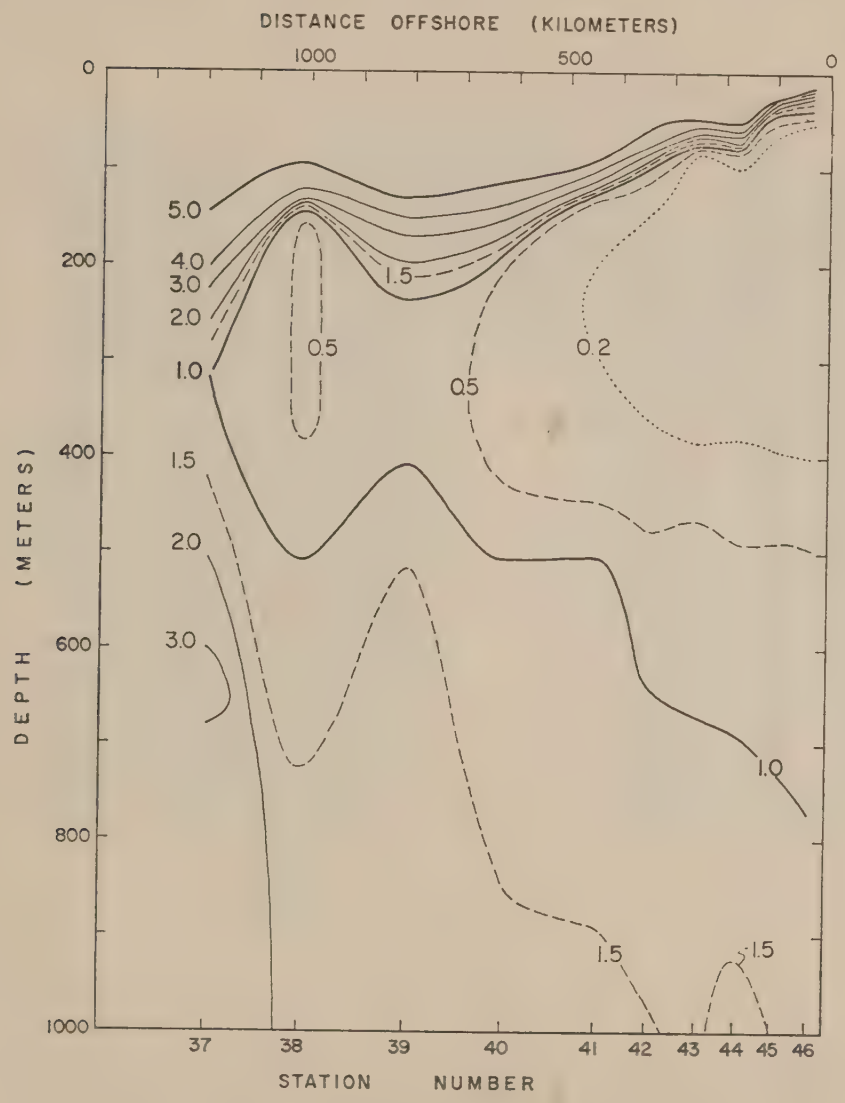

Figure 13. Distribution of dissolved oxygen (ml/L) on Profile IV; see Fig. 2 for location.

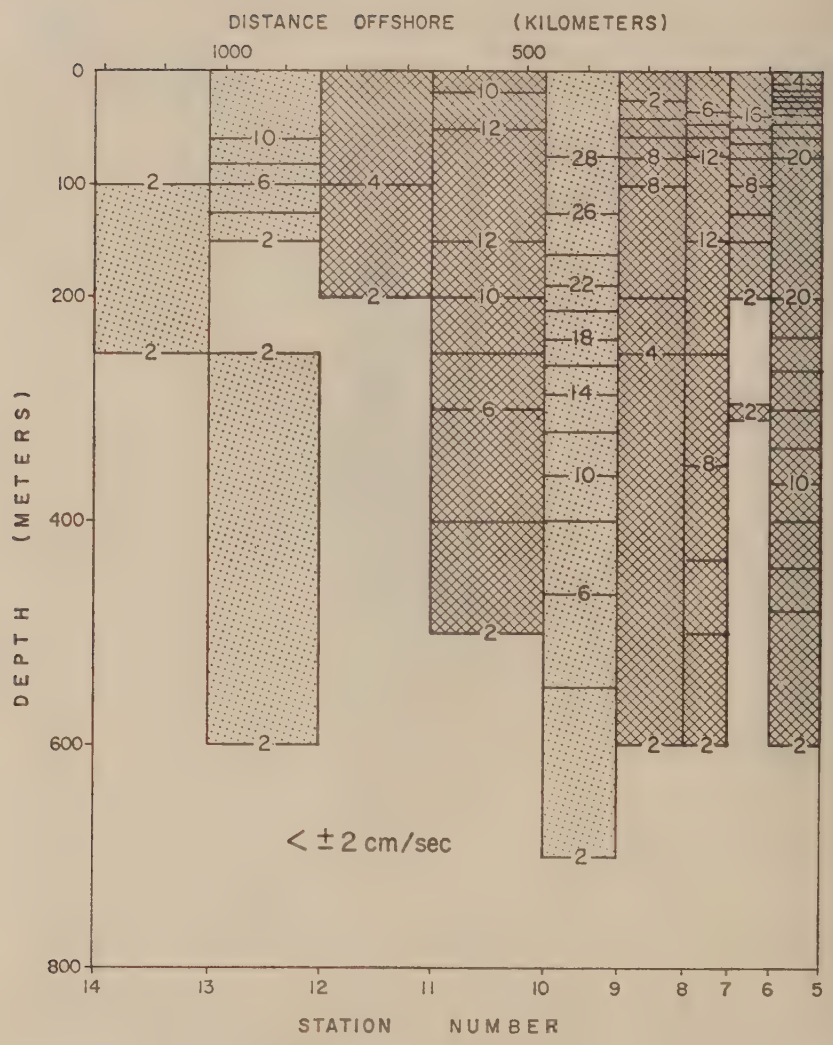

Figure 14. Geostrophic speed (cm/sec) perpendicular to Profile I; see Fig. 2 for location. Darker shading represents southward motion.

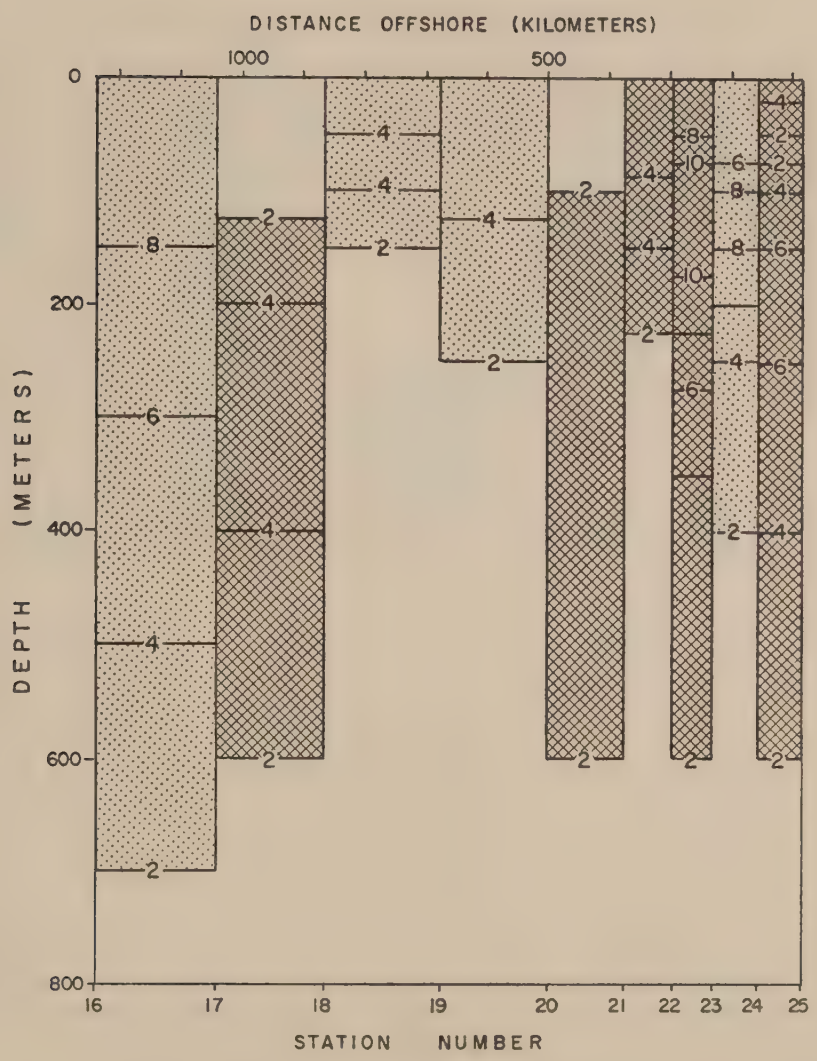

Figure 15. Geostrophic speed (cm/sec) perpendicular to Profile II; see Fig. 2 for location. Darker shading represents southward motion.

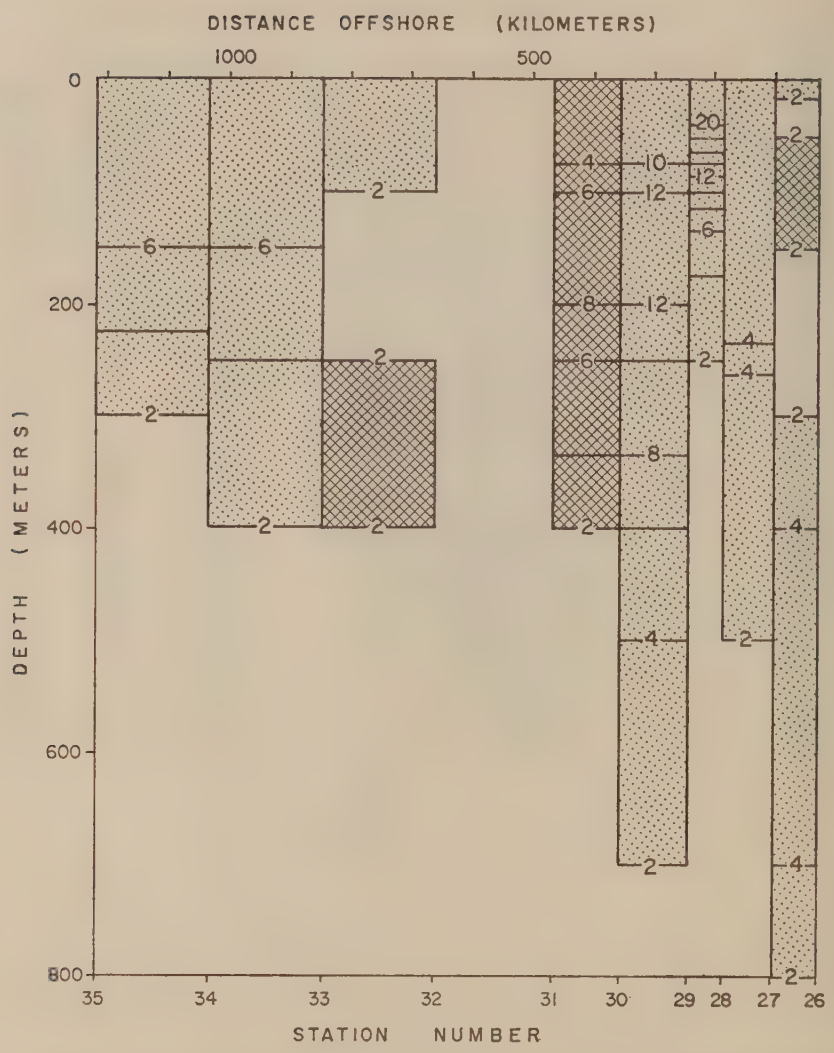

Figure 16. Geostrophic speed (cm/sec) perpendicular to Profile III; see Fig. 2 for location. Darker shading represents southward motion.

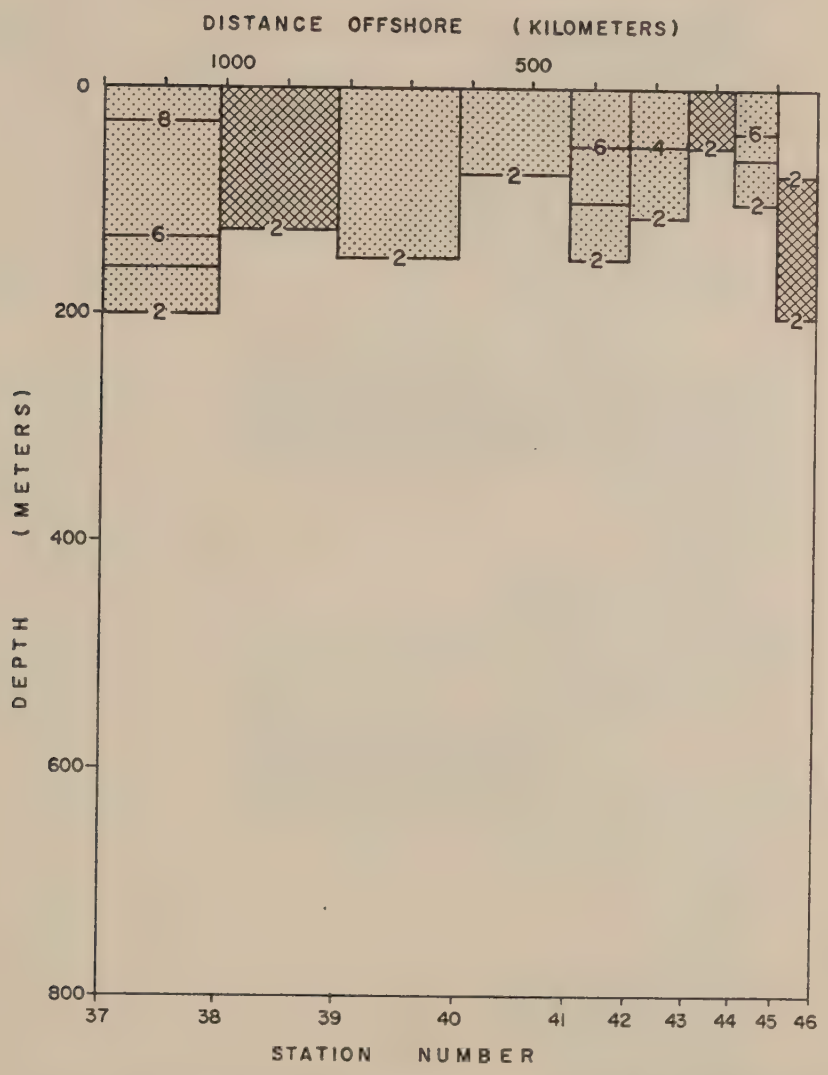

Figure 17. Geostrophic speed (cm/sec) perpendicular to Profile IV; see Fig. 2 for location. Darker shading represents southward motion.

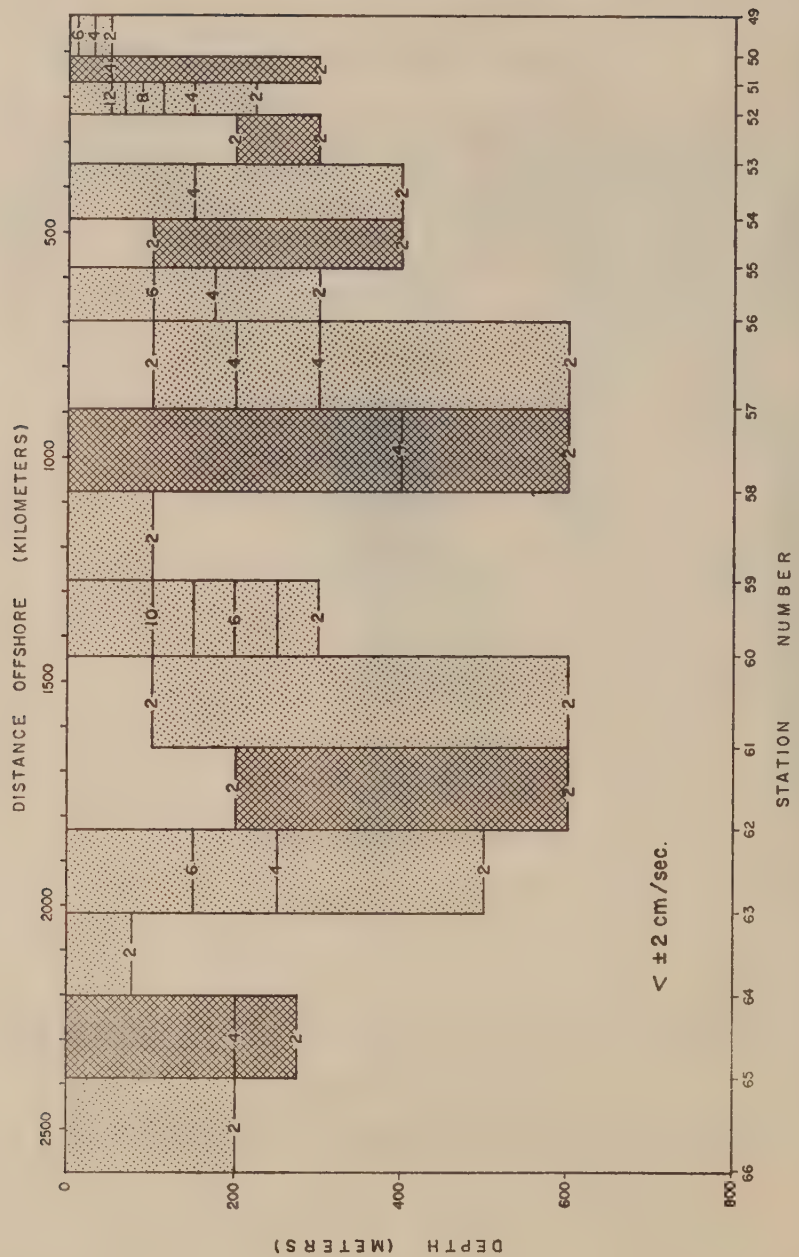

Figure 18. Geostrophic speed (cm/sec) perpendicular to Profile V; see Fig. 2 for location. Darker shading represents southward motion.

1. Flow originates off northern Peru, in the region of the boundary of the Peru Current or farther north, and extends at least as far south as 41°S at depths of several hundred meters.

2. Speed and transport of the geostrophic flow decrease from north to south. The geostrophic and measured speeds (4–10 cm/sec) are, in general, compatible except on the northernmost profile where the geostrophic speed (20 cm/sec) is significantly higher.

3. At its coastal edge, the flow closely parallels the edge of the continental shelf. On the northern profiles, principal flow appears to separate from the coast.

4. South of about 15°S, waters of the undercurrent are characterized by relatively high salinity and temperature and low oxygen content. Off southern Chile the undercurrent is also evidenced by phosphate and silicate maxima.

The strong southward flow observed on the northernmost geostrophic profile suggests that there is a supply of warm, high-saline water from the equatorial region north of the Peru Current regime. Between there and 15°S, the undercurrent is presumably associated with the boundary processes of upwelling and related enhanced vertical mixing. The significant decrease in transport of the geostrophic current from Profiles I to III suggests that much of the water may be brought to the surface in the upwelling process in addition to that lost by zonal transport.

The surface geostrophic flow to the south on the inshore end of Profile I does not appear to be compatible with the motion of the surface drogue (Fig. 9) or with the presence of upwelling. The high surface phosphate content (2.05 μg at/L) as well as the vertical distribution of density and other properties there suggest that vigorous upwelling may have occurred just prior to our observations. There is little evidence of upwelling on Profile II, but the inshore end of Profile III shows clearly all the usually accepted indications of the process.

It should also be noted that the flow measured with the parachute drogues and the flow estimated from the distribution of mass, although related, are not the same. In general, the drogue measurements were close to shore in relatively shallow water and pertained to rather specific time intervals and layers of water. The geostrophic currents, computed from the station pairs lying farther offshore in deeper water, involve a certain averaging of conditions over distances of 40 miles or more. In the immediate vicinity of the boundary, the geostrophic approximation may not be applicable because of its neglect of frictional forces, accelerations and vertical velocity.

South of 15°S, on Profiles IV and V, there are no indications of upwelling. This is in agreement with the findings of Wooster and Reid (in press) who showed that except in winter, there is little or no Ekman transport offshore between 15° and 30°S. In this region an overflow of low-salinity water from the coastal current off Chile and the presence at depth of cold, low-salinity water make the undercurrent apparent as a layer of high salinity.

Despite the relatively small volume of southward flow, particularly south of 15°S, waters with the characteristics of the undercurrent are widespread. Nothing is known concerning seasonal variations in the strength of southward flow, and it is conceivable that this may be stronger at some other time of year than October. A few of the drogue measurements suggest that stronger flow is present than is indicated by the geostrophic data. It is also possible that even a slow, and possibly intermittent, subsurface flow may be capable of developing the observed distributions of properties. Certainly the decrease in volume of southward flowing water mentioned above suggests a continual loss through vertical and horizontal transport.

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APPENDIX

Accuracy of Parachute Drogue Measurements

In estimating the absolute motion of water at a certain depth by means of parachute drogues, one is faced with (1) errors in determining the uncorrected motion of a drogue relative to the reference point, and (2) errors in positioning of the reference point itself. In addition there may be systematic errors in the correction of the apparent relative motion for the drag forces acting on the drogue system. We have considered as unimportant for the present problem the uncertainty of the magnitude of these drag forces and have accepted the empirical values of Brown (in press) without modification.

In determining the motion of a drogue relative to the reference point, the primary errors are in range and bearing as measured by radar. The inherent accuracy of the equipment itself is high, but random errors arise from operator interpretation of the radar targets. Such errors depend on operator experience, sea state, condition of the drogue's radar reflector, tuning of the radar set, etc. A measure of these errors can be obtained from analysis of the duplicate readings of range and bearing of the reference point, customarily taken every half hour or so while on a drogue station.

The within-replicate variance, σ^2, for a large number of replicates is estimated by the equation

$$\sigma^2 = \frac{\sum (x - y)^2}{2n},$$

where x and y represent the replicate values and n the number of replicate sets used in the analysis. The results of such analyses for each drogue station are included within the total error presented in Table I.

These errors can be assumed to be independent of range. The total error in positioning the drogue relative to the reference is the sum of the errors in positioning the ship (S) relative to the reference (R), and the drogue (D) relative to the ship. The S–R relation is determined from the mean of duplicate measurements of range and bearing, the S–D relation by a single measurement; the total error in the drogue position, E, is given by

$$E = 2\sqrt{\frac{\sigma^2}{2} + \sigma^2} = \sigma\sqrt{6}.$$

Estimates of total error are presented in Table I.

Errors in positioning the reference point depend on whether an island or a deep parachute drogue was employed. In the former case, the island is not a point target and may appear to shift in position when viewed from different bearings. The islands selected in this study were small and precipitous and at a sufficient distance so that we feel such errors can safely be neglected.

When it was necessary to use deep (1000 m) parachute drogues as references, the radar reflector was essentially a point target, but the assumption of negligible motion at such depths may not be valid. On one station (6°S) a rough estimate of reference drogue motion was made by bringing the ship alongside the reference drogue on three occasions and by determining the ranges and bearings of four points on the shore. Although these shore points were not ideal for this purpose, the successive measurements showed an average southward movement of 1–2 cm/sec. No correction has been made for this apparent change in reference position, but such a correction would serve to increase slightly the estimated speed of the undercurrent.

In treating all of the drogue data it was assumed that all ranges and bearings of a given set were measured simultaneously. In practice, 5–6 minutes were required for the measurements, during which the ship may have drifted approximately 70 m (20 cm/sec for 6 min). Since the ships position relative to the reference was determined by averaging measurements at the beginning and end of the set, the drift error was of the order of 35 m, a small value relative to other errors.

The final positioning of the drogue depends on the coupling of the reference point-ship vector to the ship-drogue vector. Because of errors in range and bearing, the probable position of the ship or of the drogue will lie somewhere within an annular area, with the difference between the concentric circles representing the error in range, and the enclosed angle between the radii representing the error in bearing. The total error in the final drogue position will result from the coupling of these areas. The result is a function, not only of the size of errors in ranges and bearings, but of the size of the angle enclosed by the two bearings. The solving of such vector coupling is a complex operation, and for simplification it was assumed that the position of the ship lay somewhere within a circular area representing both error in range and error in bearing. The coupling of two such circular areas is independent of the angle enclosed by the bearing. The larger of the two errors resulting from range and bearing determinations was taken as the radius of the circular area. Provided that the two errors differ by at least 15%, the situation at all stations, such an assumption will result in an overestimation of the error in final drogue position and is therefore considered justified.

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PART 4

I. ICNAF Mesh Regulations, Operation of 10% Annual Exemption October 1, 1957, through September 30, 1959

BY LAWRENCE H. COUTURE, F.R.B.

The United States Bureau of Commercial Fisheries, Fish and Wildlife Service, issued 23 exemption certificates during the first year, and 23 additional certificates during the second year to U. S. vessels. These certificates were issued by month and year as follows:

Month	Year	Certificates
October	1957	6
November		3
December		2
January	1958	3
February		4
March		2
April		1
May		1
August		1
	Total—1st 12 months	23
October	1958	5
December		1
January	1959	8
February		2
April		1
May		2
June		2
August		1
September		1
	Total—2nd year	23

At the completion of the first year, eight certificates expired and were not renewed by the vessel owners. Two certificates were revoked for failure to submit required reports.

During the second year, three certificates expired and were not renewed by the vessel owners. One certificate was cancelled when the vessel was sold. On October 1, 1959, there remained 322 certificates in effect.

Tonnage classes of exempted vessels:

Gross tons	Class	Number of Certificates As of Sept. 30, 1958	Number of Certificates As of Sept. 30, 1959
0-25	OTS	1	0
26-50	OTS	5	9
51-100	OTM	7	12
101-150	OTM	2	4
151-200	OTL	7	6
Over 200	OTL	1	1
		23	32

The landings of these vessels are presented in the attached table 1.

TABLE 1 - Summary of the Operation of the 10% Annual Exemption.

SUBAREA 3

		1st Year		2nd Year	
		No.	%	No.	%
Exempted vessels[1]					
Fishing trips		9		27	
All species	000 lb.	2,107	100.0	5,724	100.0
Haddock	,, ,,	0	0	28	0.5
Cod	,, ,,	0	0	9	0.2
Redfish	,, ,,	2,106	99.9	5,599	97.8
Other species[2]	,, ,,	1	0.1	88	1.5
No. of trips with haddock		0		3	
No. of trips with cod		0		3	
No. of trips with redfish		9		27	
Range of haddock landings per trip, lb.		—		275-16,800	
Range of cod landings per trip, lb.		—		90- 6,900	
Excess trips[3]		0		0	
Pounds excess haddock[4]	000 lb.	0		0	
Pounds excess cod[4]	,, ,,	0		0	

1) Operating under 10% annual exemption certificates.
2) Other species includes halibut, white hake, cusk, pollock, flounders, and silver hake.
3) Trips of more than 5.000 pounds and more than 10% haddock or cod.
4) Quantity of haddock or cod in excess of that covered by trip exemptions.

SUBAREA 4

		1st Year		2nd Year	
		No.	%	No.	%
Exempted vessels[1]					
Fishing trips		70		102	
All species	000 lb.	11,840	100.0	14,864	100.0
Haddock	,, ,,	374	3.2	1,136	7.6
Cod	,, ,,	34	0.3	171	1.1
Redfish	,, ,,	11,247	95.0	12,761	85.9
Other species[2]	,, ,,	185	1.5	796	5.4
No. of trips with haddock		24		61	
No. of trips with cod		21		61	
No. of trips with redfish		68		89	
Range of haddock landings per trip, lb.		200-89,300		200-100,200	
Range of cod landings per trip, lb.		35-6,550		80-11,700	
Excess trips[3]		4		19	
Pounds excess haddock[4]	000 lb.	108		865	
Pounds excess cod[4]	,, ,,	0		4	

1) Operating under 10% annual exemption certificates.
2) Other species includes halibut, white hake, cusk, pollock, flounders, and silver hake.
3) Trips of more than 5,000 pounds and more than 10% haddock or cod.
4) Quantity of haddock or cod in excess of that covered by trip exemptions.

SUBAREA 5

		1st Year		2nd Year	
		No.	%	No.	%
Exempted vessels[1]					
Fishing trips		628		1,304	
All species	000 lb.	23,178	100.0	41,206	100.0
Haddock	,, ,,	2,453	10.6	2,404	5.8
Cod	,, ,,	471	2.0	670	1.6
Redfish	,, ,,	7,333	31.6	12,552	30.5
Other species[2]	,, ,,	12,921	55.8	25,580	62.1
No. of trips with haddock		534		841	
No. of trips with cod		539		784	
No. of trips with redfish		265		454	
Range of haddock landings per trip, lb.		15-113,000		10- 63,800	
Range of cod landings per trip, lb.		10- 20,650		10- 23,035	
Excess trips[3]		154		101	
Pounds excess haddock[4]	000 lb.	1,146		1,012	
Pounds excess cod[4]	,, ,,	68		84	

1) Operating under 10% annual exemption certificates.
2) Other species includes halibut, white hake, cusk, pollock, flounders, and silver hake.
3) Trips of more than 5,000 pounds and more than 10% haddock or cod.
4) Quantity of haddock or cod in excess of that covered by trip exemptions.

ALL SUBAREAS

		1st Year		2nd Year	
Subarea		No.	%	No.	%
Exempted vessels[1]		23		32	
Fishing trips		707		1,433	
All species	000 lb.	37,125	100.0	61,794	100.0
Haddock	,, ,,	2,827	7.6	3,568	5.8
Cod	,, ,,	505	1.4	850	1.4
Redfish	,, ,,	20,686	55.7	30,912	50.0
Other species[2]	,, ,,	13,107	35.3	26,464	42.8
No. of trips with haddock	,, ,,	558		905	
No. of trips with cod		560		848	
No. of trips with redfish		342		570	
Range of haddock landings per trip, lb.		15-113,000		10-100,200	
Range of cod landings per trip, lb.		10- 20,650		10- 23,035	
Excess trips[3]		158		120	
Pounds excess haddock[4]	000 lb.	1,254		1,877	
Pounds excess cod[4]	,, ,,	68		88	

1) Operating under 10% annual exemption certificates.
2) Other species includes halibut, white hake, cusk, pollock, flounders, and silver hake.
3) Trips of more than 5,000 pounds and more than 10% haddock or cod.
4) Quantity of haddock or cod in excess of that covered by trip exemptions.

XI. United States Research in the Convention Area during 1959

A. BY HERBERT W. GRAHAM

LABORATORY DIRECTOR, BUREAU OF COMMERCIAL FISHERIES

BIOLOGICAL LABORATORY, WOODS HOLE, MASS.

SUBAREA 5[1]

Haddock (*Melanogrammus aeglefinus* (L.))

The Fishery. U. S. haddock landings were lower again this year, continuing the trend begun in 1957 (see Table 1). There was an increase in effort but a slight decrease in the catch per unit of effort. As had been anticipated, there was not a strong recruitment of 1956 year-class fish (about 29% of the total catch) and the large 1954 year-class was still contributing significantly (about 13% of the total catch).

Evaluation of the Mesh Regulation. The 1952 year-class of haddock has now virtually passed through the fishery, making possible a new evaluation of the Subarea 5 mesh regulation. The 1952 year-class was fished almost entirely with the regulation ($4\frac{1}{2}$-inch) cod-end mesh. Through age 5, the 1948 year-class (fished with small mesh nets) and the 1952 year-class yielded nearly equal numbers of fish. However, landings from the 1952 year-class weighed almost 20% more than landings from the 1948 year-class. This difference is considered to be the result of mesh regulation.

[1]) Most of U.S. research was restricted to Subarea 5. Studies conducted in other subareas are included in this report with appropriate reference to region concerned.

TABLE 1. Trends in the Subarea 5 Haddock Fishery[1].

Year	Large	Scrod	Total	Days fished	Catch/Day
1956	55.6	52.3	107.9	7763	13.9
1957	51.4	49.5	100.9	9090	11.1
1958	43.1	38.4	81.5	9261	8.8
1959[2]	42.2	36.0	78.2	8455	8.3

1) Landings in millions of pounds.
2) Based on a preliminary analysis.

Young-of-the-Year Survey. Surveys of young-of-the-year (or pre-recruit haddock) have been made for several years now. These surveys are concerned with Subarea 5 and Subdivision 4X. Approximately one month of sea time is devoted to surveying the banks to assess the strength of young-of-the-year and 1-year-old haddock. In general these surveys have yielded data on pre-recruit abundance that has subsequently been verified, in magnitude at least, by the landings of the commercial fleet. Although no unusually large year-class has yet been detected, some amelioration of the downward trend of the past few years is expected on the basis of the surveys made in 1958 and 1959.

Age Determination. The techniques and validity of aging haddock, using scales, have been carefully re-examined and a report on this study will soon be ready for publication. The validity of the scale aging method through the first years of life for Georges Bank haddock is now regarded as being established beyond a reasonable doubt. Further studies on the aging problem using techniques other than the scale method are progressing satisfactorily.

Ecology. The study of the haddock's ecology on particular grounds, mentioned in last year's research report (1958), is progressing satisfactorily. Studies of the seasonal changes in gonads and other organs are also under way. Of particular interest is the seasonal change in liver weight and its inverse relationship to gonad weight. There is evidence that the developing gonads depend largely on reserves held in the liver, as well as material from other parts of the body.

Cod (*Gadus morhua* L.)

The Fishery. Total U. S. landings for 1959 were up about 2 million pounds over the 1958 total of 27 million pounds. This was principally due to an increase in the abundance of market cod (fish from $2\frac{1}{2}$ to 10 pounds). The 1958 increase was due to the presence of unusually large numbers of scrod fish (fish of less than $2\frac{1}{2}$ pounds).

Research. In collaboration with the Woods Hole Biological Laboratory, two U. S. Navy airships (blimps) dropped drift bottles over an area of more than 10,000 square miles of ocean surface in one night (February 1959). The resulting drift data will help to clarify the nature of surface currents off the coast of New Jersey and the effect of these currents on the fate of eggs and larvae of the codfish that spawn here.

Further analysis of tag returns has yielded some valuable comparative data on the types of tags that have been used. Petersen disc tags with the pin applied through the dorsal musculature give better results in terms of returns than the modified Lea tags previously used, regardless of the time at large.

A study of the emigration of the larger cod to colder waters in Subarea 4 and 5 has been completed.

Redfish (*Sebastes marinus* (L.))

The U. S. redfish landings in 1959 were about 137 million pounds, 10 million pounds less than 1958 and the second lowest amount since 1946. This continues the trend of gradual decline in redfish landings since reaching a peak in 1951. About 29 million pounds of this year's total were

caught in the Gulf of Maine, 50 million on the Nova Scotian banks, 38 million on the Grand Bank, and 20 million in the Gulf of St. Lawrence. The Labrador coast fishery that was opened in 1958 did not develop as anticipated this year.

The Gulf of Maine redfish fishery remains fairly constant in abundance with an average catch of close to 10 thousand pounds per day in 1959. On the Grand Bank and Nova Scotian banks fishing effort increased slightly while catch-per-day decreased about 10% from the 1958 values, ranging between 21 and 33 thousand pounds per day on different grounds. Fishing effort decreased in the Gulf of St. Lawrence while the catch-per-day rose slightly to 21 thousand pounds.

Research. Field work was concentrated on the inshore stock of redfish at Eastport, Maine. Routine sampling of the commercial landings at the four major redfish ports was continued for length, age and abundance analyses, and for spawning, racial, and parasite studies.

Kelly reported on three aspects of his work at the Redfish Symposium at Copenhagen in October.

The measurement of a long series of meristic and morphometric characteristics designed to clarify the status of subspecies of *Sebastes marinus* did not show a clear separation between *marinus*-type and *mentella*-type redfish. Diameter of orbit was the most variable morphometric characteristic, but the measurements did not separate the fish into two groups of large-eyed and small-eyed fish. Instead, at least four modal peaks of eye size were present in the combined sample from all areas studied, suggesting that more comprehensive sampling may disclose a normal distribution of eye size for the whole *Sebastes* population.

There was a wide range in the average length of redfish sampled from different areas. Despite the differences in length range and eye size, there was very little difference in meristic characteristics, the differences suggesting a possible clinal distribution of meristic characteristics in the whole North Atlantic population.

Mid-winter sampling of young redfish (10 to 60 mm) in the Gulf of Maine has revealed some important information on the duration of the pelagic period and the growth and vertical distribution of the larvae during that time. Newly spawned young (5 to 6 mm) appear at the surface in the spring. As they grow to 10-15 mm the larvae move down into the thermocline, remaining there until about 25 mm in length. Beyond this size they move even deeper into cooler water where they live until they reach an average length of 50 mm and then move to the bottom. The pelagic period is about 5½ months in duration, long enough to permit the young fish to drift long distances with the water currents.

Study of the inshore stock of redfish at Eastport, Maine, has provided observation of the live fish in its natural environment. Recapture of a great many tagged fish at the tagging site reveals a rather strong territorial instinct and little tendency to migrate. Otolith studies show the growth of tagged fish to be much slower than the growth rate before tagging. Tagging altered the pattern of zone formation in the otolith so that virtually no opaque material was deposited for as long as 3 years after tagging.

Flounder Studies.

The Fishery. Landings of yellowtail in 1959 were again high, about 28 million pounds, though slightly lower than in 1958 when about 32 million pounds were landed. Apparently the strong year-classes from 1955 and 1956 are now passing out of the fishery. Approximately 24 million pounds of other species of flounders were also landed in 1959.

Research. An analysis of relative abundance (catch per unit of effort) of yellowtail flounder, *Limanda ferruginea*, has been completed for the three principal New England fishing grounds.

In addition, 3000 yellowtail were tagged in 1959 to further define movements and estimate fishing mortality.

Silver Hake.

The Fishery. Total annual landings of silver hake from New England grounds was 85

million pounds, approximately the same as the previous year. The occurrence of smaller fish on the offshore grounds focused the fishing effort on to the larger silver hake located inshore.

Research. Data collected on cruises increased our knowledge of the seasonal distribution of this species. The deep water between 100 and 200 fathoms appears to be the wintering area for some if not most of the silver hake. Cruises made in Subarea 5Z show that the silver hake intermingle with the deep-water species *Merluccius albidus* during the winter, but separate and move inshore during the summer months. Specific collections are being made of both species to determine the biological and ecological relationship of the two species.

Industrial Fishery.

The landings of non-food species of trawl fishes for reduction to meal stopped in September 1959 due to economic factors. As a result, a 4-year continum of fishery data on certain mixed groundfish populations also came to an end. These data are now being analyzed.

Sea Scallops (*Placopecten magellanicus* Gmelin)

The Fishery. U. S. landings from the Convention Area in 1959 were 18.7 million pounds, an increase of 11% over the 1954-1958 average and an increase of 25% over 1958. Fishing effort was 8480 days, down 19 percent from the 1954-1958 average and down 3% from 1958. The newly recruited year-class made up over 60% of the catch. The catch per tow was very high. Either the new year-class was unusually abundant or was more densely aggregated than in previous years.

Research. Growth and mortality rates calculated during the year all reinforce the previous conclusion that postponement of first capture would result in a substantial increase in the yield of a year-class.

Benthos Investigations.

A report describing the Georges Bank groundfish food resources is now being prepared, the quantitative as well as the qualitative aspects being considered. Bottom sediments, which strongly influence many groundfish foods, are also being studied. A survey of Georges Bank bottom sediments has been completed, and this work is now being extended to include the southern Gulf of Maine and Browns Bank. Field work for part of this extended coverage was completed last August.

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FOOD HABITS OF LARVAL COD, HADDOCK, AND COALFISH IN THE GULF OF MAINE AND GEORGES BANK AREA

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Food Habits of Larval Cod, Haddock, and Coalfish in the Gulf of Maine and Georges Bank Area

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Introduction

One of the many factors which may influence the survival of larval fish is the availability of suitable food. European investigators (LEBOUR, 1919; OGILVIE, 1938; and WIBORG, 1948) have observed that pelagic fish larvae are at times selective in their choice of food. A definite preference for a specific food form is sometimes indicated, although much of the selectivity is due to the size relationship of the larval fish and the available zooplankton.

In this paper, stomach analysis data are presented which demonstrate the relation of the food organisms and their size to larval gadoids. To avoid confusion, all the fish considered, ranging in size from 4 mm to 68 mm, are referred to as larval fish. Three species of gadoids are considered; cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; and coalfish, *Pollachius virens*.

Methods

The North Atlantic Fishery Investigations of the US Fish and Wildlife Service conducted surveys of the Gulf of Maine/Georges Bank area (Fig. 1) in the springs of 1953, 1955, 1956, and 1957 in order to measure the relative abundance of fish eggs and larvae and to relate their distribution and mortality to hydrographic conditions.

The principal plankton collecting gear used during these surveys was the Hardy Plankton Recorder. Simultaneous samples of zooplankton and fish larvae were collected from the surface with a standard one-metre net at 12 hour intervals for hatching and identification purposes. Bolting silk number 0 with an aperture of 0·57 mm was used in the metre net. This silk size retains all fish eggs and larvae endemic to the Gulf of Maine but not all of the smaller zooplankton forms. SAVILLE (1958) shows quite clearly the selectivity of various mesh sizes in plankton nets.

All larval fish and other zooplankton from the metre net tows were preserved

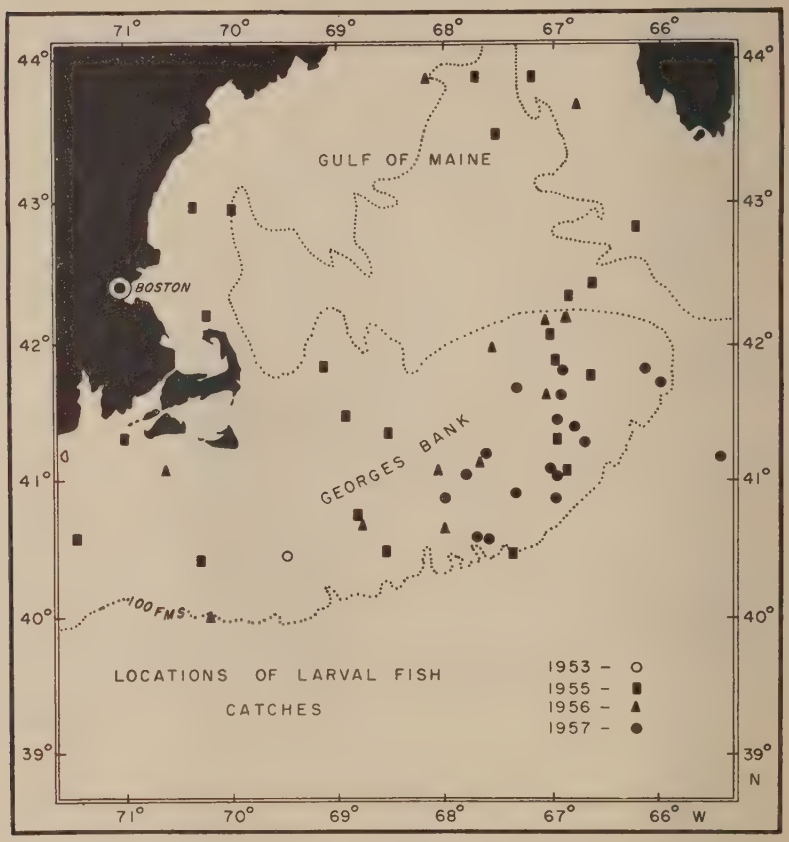

Figure 1. Locations of larval fish catches.

in 5% formalin. Because the emphasis of this paper is on the food of the larval fish and because the samples of these fish obtained from the tows were small, it was practical and convenient to combine the data from all the tows and cruises for each year studied. The only exception to this was in the one tow made in May 1956 in Great Harbor, Woods Hole, for comparison of the food of inshore fish with those from off shore.

The stomachs of the fish were dissected out, opened and examined grossly under low power (10×). The final sorting of organisms was done at 45×. For specimens less than 10 mm, which do not have a well defined stomach, it was necessary to examine the whole gut under 100×.

The stomach contents were identified and counted, and an estimation of the percentage volume of the different foods was made. Volumes of the zooplankton caught in the net were measured by displacement. *Centropages typicus* and *Centropages hamatus* were combined as *Centropages; Pseudocalanus minutus* and *Paracalanus parvus* as "*Pseudocalanus*-type". All stages

Table 1

Stomach contents of larval fish – "Albatross III" Cruise 61, May 1955; 75, May 1956

Cruise No. and tow No.	Location	Species	Size (mm)	Number of fish	Food
61–2	41°53′N	Haddock	10	1	Larval copepod remains
	66°59′W	Coalfish	22–24	3	*Calanus*, *Centropages*, larval copepods
61–5	43°29′N	Coalfish	19	1	Larval copepods
	67°29′W				
61–10	41°49′N	Coalfish	28–35	5	*Calanus*, "*Pseudocalanus*-type", larval euphausiids, larval copepods, unrecognizable remains
	69°06′W				
61–11	41°23′N	Haddock	21	1	"*Pseudocalanus*-type", *Calanus*
	68°28′W	Coalfish	13–24	3	"*Pseudocalanus*-type", *Calanus*, larval euphausiids
61–13	40°28′N	Haddock	7–16	4	Larval euphausiids, larval copepods, *Evadne*, gastropod larvae
	68°30′W				
61–16	40°26′N	Haddock	13	1	Larval copepods, *Calanus* (young)
	70°15′W				
61–17	40°32′N	Haddock	11, 25	2	"*Pseudocalanus*-type", larval copepod remains, larval euphausiids
	71°24′W	Coalfish	25, 26	2	Larval copepods
75–1	40°00′N	Haddock	4–7	5	Larval copepods
	70°12′W				
75–5	43°43′N	Coalfish	30, 33	2	*Calanus*, fish eggs, unrecognizable matter
	66°46′W				
75–7	43°50′N	Coalfish	26, 29	2	*Calanus*, *Temora*, larval copepods, larval euphausiids
	68°10′W	Cod	9–13	3	"*Pseudocalanus*-type", larval copepod remains
75–13	42°10′N	Cod	11–16	3	"*Pseudocalanus*-type", larval copepods, invertebrate eggs
	67°02′W	Coalfish	21–28	2	*Calanus*, "*Pseudocalanus*-type"
75–17	41°07′N	Cod	6–9	20	Larval copepods, invertebrate eggs, phytoplankton
	67°40′W	Haddock	6–9	20	Larval copepods, invertebrate eggs, phytoplankton, *Calanus* (young), pelecypod larvae
75–21	40°08′N	Haddock	25–46	5	"*Pseudocalanus*-type", *Temora*, *Centropages*, *Evadne*, *Oithona*, *Calanus*, larval amphipods, fish eggs
	72°00′W				

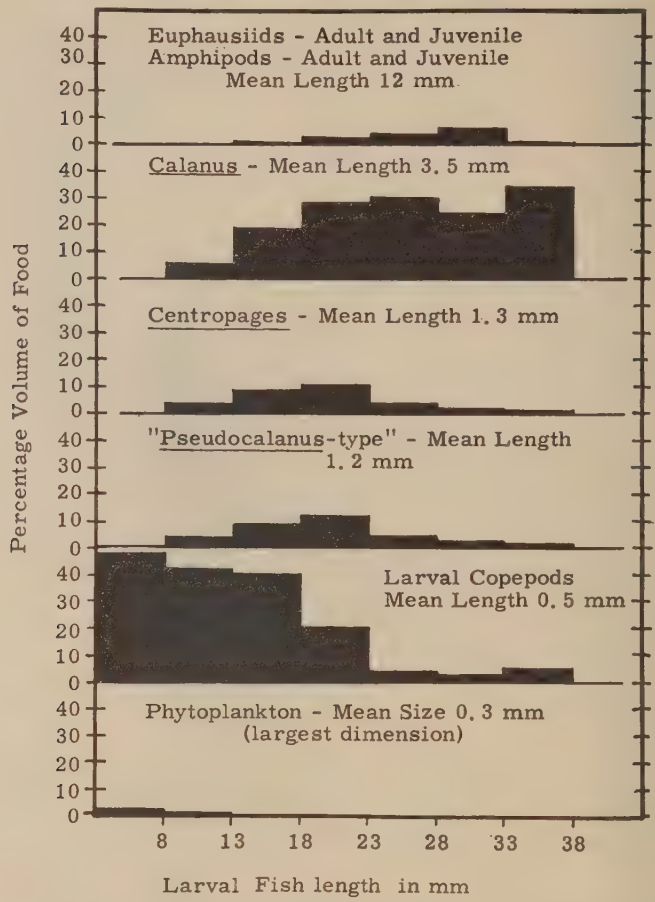

Figure 2. Percentages by volume of major types of food eaten by different size groups of larvae – 1953, 1955, 1956, 1957.

of copepods up to 0·5 mm length, euphausiids up to 8·0 mm length, and amphipods up to 6·0 mm length are listed as larvae. Because the diets of the three species are essentially similar (Table 1), especially with respect to the relation of size of larva to size of food organism, and because the diversity of times and places of collection preclude precise comparisons, data for the three gadoid species are grouped in some instances.

Results

1. Stomach contents

The most important factor in the feeding habits of the larval fish is the size of the available prey. Sizes of common food organisms are given in Table 2. As the length of the fish increases, there is generally an increase in the size

Table 2

Average length of organisms taken as food in 1953, 1955, 1956, 1957

	Average length (mm)
Copepods	
Calanus finmarchicus	3·5
Pseudocalanus minutus	1·2
Paracalanus parvus	0·8
Centropages typicus	1·3
Centropages hamatus	1·1
Metridia lucens	2·3
Temora longicornis	1·2
Eurytemora herdmani	1·2
Acartia clausi	1·0
Tortanus discaudatus	1·7
Oithona similis	0·7
Eggs and larval stages	<0·5
Harpacticoids	0·7
Euphausiids	
Meganyctiphanes norvegica	20·0
Thysanoessa inermis	11·0
Eggs and larval stages	<8·0
Amphipods	
Euthemisto compressa	15·0
Hyperia galba	12·0
Hyperia medusarum	12·0
Eggs and larval stages	<6·0
Isopods	
Juveniles	3·0
Cumacea	3·5
Cladocera	
Evadne sp.	0·9
Gastropod larvae	0·2
Pelecypod larvae	0·2
Fish eggs	0·8
Fish larvae	7·0
Diatoms	0·3

of the food taken (Fig. 2). This relationship holds true for all years studied and for almost all items of food. (In the tables subsequent to Table 2, all food items are listed in order of increasing size.)

1953. During 1953, only one tow yielded appreciable numbers of fish. These 112 fish ranged in size from 9 to 28 mm. Seventy-five per cent. of the food taken by the 9 to 13 mm size group was larval copepods while *Centropages* made up the bulk of the food of the larger sizes (Table 3).

1955. The major portion of the food taken by the smallest fish (4–8 mm) was larval copepods, while the identifiable diet of the larger fish was mostly juveniles and adults of *Calanus* and "*Pseudocalanus*-type". *Centropages* contributed only 1% of the total food of all larvae (Table 4) as opposed to 54% in 1953.

1956. Stomach contents taken from 104 fish from Georges Bank and Gulf of Maine area and 119 fish caught in Great Harbor, Woods Hole, were examined. The food of the first group was a little more varied than in previous years although *Calanus* and larval copepods still comprised the bulk of the diet. As in 1955, *Centropages* made up about 1% of the food eaten. Small amounts of phytoplankton and appreciable numbers of invertebrate eggs were in the stomachs of the 4 to 8 mm size group.

Table 3

Percentage composition of stomach contents of haddock larvae from Georges Bank, 1953

	Length groups of fish (mm)						
	9–13	14–18	19–23	24–28	29–33	34–38	Total
Number of larvae	4	31	44	24	8	1	112
Phytoplankton	1	0	0	0	0	0	<1
Larval copepods	75	38	27	9	9	10	28
Temora longicornis	0	2	3	2	0	0	1
Centropages	13	42	47	64	66	90	54
Metridia lucens	0	4	1	5	9	0	3
Calanus finmarchicus	3	4	12	10	9	0	6
Amphipods	0	0	0	0	3	0	<1
Euphausiids	0	3	10	10	4	0	5
Unrecognizable	12	7	0	0	0	0	3
% empty	0	6	2	4	13	0	7
% with *Caligus*[1])	0	42	73	71	75	100	60

[1]) Ectoparasite

Table 4

Percentage composition of stomach contents of gadoid larvae, 1955

	Length groups of fish (mm)							
	4–8	9–13	14–18	19–23	24–28	29–33	34–38	Total
Number of larvae	24	11	22	35	23	8	3	126
Gastropod larvae	<1	0	0	0	0	0	0	<1
Larval copepods	93	17	4	1	5	3	17	20
Evadne sp.	<1	0	0	0	0	0	0	<1
Pseudocalanus	4	6	14	14	5	14	7	9
Fish eggs	0	0	2	1	1	0	0	1
Centropages	0	0	0	2	8	0	0	1
Calanus finmarchicus	0	26	69	77	62	50	53	48
Euphausiid larvae	2	0	0	0	2	8	0	2
Unrecognizable	0	51	11	5	17	25	23	18
% empty	4	36	22	14	0	0	0	12
% with *Caligus*[1])	0	9	9	9	26	0	33	10

[1]) Ectoparasite

The fish from Woods Hole harbour were larger than those from off shore, and their stomach contents were slightly different. *Tortanus discaudatus*, which was not present in the stomachs of the offshore fish, made up 29% of the food of the Woods Hole fish. *Centropages*, *Temora longicornis*, and larval amphipods were the other dominant food forms (Tables 5 and 6).

1957. As in 1955 and 1956, the smaller larvae were feeding almost exclusively on larval copepods. The larger fish utilized mostly juvenile and adult *Calanus* and *Centropages* (Table 7).

2. Species composition in stomachs and in metre net

In order to determine if the fish larvae are selective in their choice of food, it is necessary to compare the species composition in the stomachs to that in the environment. Such comparisons for haddock caught on Georges Bank in 1953 and coalfish caught in Woods Hole in 1956 are shown in Table 8.

Table 5

Percentage composition of stomach contents of gadoid larvae – Georges Bank, 1956

	Length groups of fish (mm)													
	4–8	9–13	14–18	19–23	24–28	29–33	34–38	39–43	44–48	49–53	54–58	59–63	64–68	Total
Number of larvae	42	24	21	3	6	4	1	0	1	1	0	0	1	104
Phytoplankton	3	0	0	0	0	0	0	–	0	0	–	–	0	<1
Pelecypod larvae	0	<1	0	0	0	0	0	–	0	0	–	–	0	<1
Invertebrate eggs	19	6	3	0	0	0	0	–	0	0	–	–	0	3
Larval copepods	69	41	37	33	0	0	0	·	0	0	–	–	0	18
Evadne sp.	0	4	0	0	0	<1	1	–	0	0	–	–	0	<1
Oithona similis	0	9	1	0	0	0	0	–	0	0	–	–	0	1
Fish eggs	0	0	0	33	1	5	0	–	5	30	–	–	0	7
"*Pseudocalanus*-type"	0	9	32	0	3	0	5	–	0	0	–	–	0	5
Temora longicornis	0	2	0	0	10	7	25	–	15	0	–	–	0	6
Centropages	0	0	0	0	1	0	0	–	0	0	–	–	0	<1
Calanus finmarchicus	0	8	23	33	44	45	15	–	15	30	–	–	0	22
Amphipod larvae	0	0	0	0	0	1	0	–	0	0	–	–	0	<1
Euphausiid larvae	0	0	0	0	0	5	0	–	0	0	–	–	0	<1
Amphipod adult	0	0	0	0	0	0	0	–	0	0	–	–	90	9
Unrecognizable	9	21	4	0	41	34	54	–	65	40	–	–	10	28
% empty	7	8	24	0	33	0	0	–	0	0	–	–	0	11
% with *Caligus*[1])	0	4	0	0	0	0	0	–	0	0	–	–	100	2

[1]) Ectoparasite

Table 6

Percentage composition of stomach contents of coalfish larvae – Woods Hole, 1956

	Length groups of fish (mm)					
	24–28	29–33	34–38	39–43	44–48	Total
Number of larvae	10	29	61	15	4	119
Evadne sp.	0	0	<1	<1	0	<1
Acartia clausi	<1	<1	<1	<1	0	<1
Eurytemora herdmani	3	2	3	2	0	2
Temora longicornis	11	10	10	11	9	10
Centropages	36	29	29	22	12	25
Tortanus discaudatus	28	29	28	26	40	29
Harpacticoids	<1	1	<1	0	0	<1
Calanus finmarchicus	<1	3	1	2	0	1
Isopod larvae	1	0	<1	<1	1	<1
Cumaceans	0	<1	0	0	0	<1
Post-larval fish	0	0	1	0	0	1
Amphipod larvae	1	1	1	5	24	6
Euphausiid larvae	1	2	2	3	0	1
Unrecognizable	18	23	23	27	14	24
% empty	0	0	0	0	0	0
% with *Caligus*[1])	20	10	23	0	0	16

[1]) Ectoparasite

Table 7

Percentage composition of stomach contents of gadoid larvae, 1957

	Length groups of fish (mm)							
	4–8	9–13	14–18	19–23	24–28	29–33	34–38	Total
Number of larvae	35	11	5	7	13	3	1	75
Phytoplankton	2	0	0	0	0	0	0	<1
Pelecypod larvae	2	0	0	0	0	0	0	<1
Gastropod larvae	3	0	0	0	0	0	0	<1
Invertebrate eggs	12	0	0	0	2	0	0	2
Larval copepods	80	75	100	43	7	0	0	44
Evadne sp.	0	3	0	0	0	0	0	<1
Pseudocalanus	0	0	0	36	13	0	0	7
Centropages	0	0	0	0	43	66	0	16
Calanus finmarchicus	0	0	0	21	30	10	100	23
Euphausiid larvae	0	0	0	0	0	8	0	1
Unrecognizable	1	22	0	0	5	16	0	6
% empty	17	27	0	0	0	0	0	12
% with *Caligus*[1])	0	0	0	14	15	33	0	5

[1]) Ectoparasite

Euphausiids and copepods which were the most abundant groups in the metre net samples in 1953 were generally most abundant in the stomachs of the haddock. Their order of abundance, however, differed. Although euphausiids were the dominant animals present, the fish were eating *Centropages* and larval copepods. The order of abundance of animals in the metre net samples in 1956 and in the stomachs of the coalfish was similar. The absence of adult amphipods and the greater percentage of *Centropages* and possibly *Temora* in the stomachs, however, indicates that the fish were somewhat selective in their feeding.

Although euphausiids were the most abundant food form in the 1953 sample, their size (approximately 20 mm) apparently excluded them from the diet of

Table 8

Comparison of zooplankton species in stomachs and in metre net hauls

Haddock – 1953 – Georges Bank			Coalfish – 1956 – Great Harbor, Woods Hole		
Species	% comp. metre net	% comp. stomach	Species	% comp. metre net	% comp. stomach
Euphausiids	50	5	*Tortanus discaudatus*	43	37
Centropages	15	55	*Centropages*	16	32
Metridia lucens	10	3	Adult amphipods	13	0
Calanus finmarchicus	10	6	*Temora longicornis*	7	13
Larval copepods	5	28	Larval amphipods	5	7
Amphipods	2	1	Larval euphausiids	4	1
Limacina retroversa	2	0	Adult euphausiids	3	0
Sagitta elegans	2	0	*Eurytemora herdmani*	3	3
Temora longicornis	1	1	*Calanus finmarchicus*	3	1
Candacia armata	1	0	*Pseudocalanus*	1	0
Fish eggs	1	0	*Acartia clausi*	1	1
Decapod zoea	1	0	*Evadne* sp.	1	1
			Post-larval fish	0	1
			Larval isopods	0	1
			Harpacticoids	0	1
			Cumacea	0	1

the larval haddock. The smallest haddock were feeding mainly on larval copepods (0·5 mm) while the larger haddock were feeding principally on *Centropages* (approximately 1·2 mm). There was a gradual increase in the percentage of *Centropages* and a decrease in the percentage of larval copepods in the stomachs with an increase in the size of the haddock (Table 3). In 1956 stomachs of coalfish taken from Great Harbor, Woods Hole, did not contain adult amphipods (12–15 mm) even though they were relatively abundant in the water. The coalfish also appeared to favour *Centropages* (approximately 1·2 mm) over *Tortanus discaudatus* (approximately 1·7 mm) as food (Table 8).

Discussion

The larval cod, haddock, and coalfish appear to select food of a certain size range varying with the size of fish. Lebour (1920) and Wiborg (1948) have suggested that it is the width of the food form and the size of the mouth and gullet of the fish rather than the length of the particular food that is important. We have observed in the laboratory that even if an animal can be taken into the mouth of a larval fish it is often too large to be swallowed.

The selectivity as to size of food can be summarized as follows. Prior to yolk sac absorption (at a length of approximately 4·5 mm) the larval fish feed upon copepod nauplii and very insignificant amounts of phytoplankton. From 4 to 13 mm the larvae eat mostly larval copepods, and from 13 to 23 mm principally small copepods (*Oithona* and *Centropages*) are consumed. Fish larger than 25 mm can utilize almost any size copepod and begin to eat young amphipods and euphausiids. Any one species is seldom singled out if there are others of the same size available. It is sometimes difficult to correlate the stomach contents with the available food as the fish are often captured in an environment differing from that in which they were feeding.

The seasonal variation in the plankton plays an important role in determining

the diet of larval and juvenile fish. LEBOUR (1920) found that one food item was usually predominant in the fish stomachs and in the water, and that the type of organism most abundant would often change as the season progressed. In the spring, in the Gulf of Maine and Georges Bank, when fish larvae of the species used in this study are most abundant, there are relatively more invertebrate eggs and larval copepods available. As the fish increase in size, there is a corresponding increase in the amount of larger food forms.

Not only does the type of food eaten vary with the size of the fish, but also the amount of food eaten. For example, the stomach of a 10 mm fish contained eight larval copepods whereas a 15 mm fish had eaten 18 *Centropages typicus*, and a 25 mm fish had eaten 50 *Centropages typicus*. Numbers, however, are not a true indication of the relative amount of food in the gut as one *Calanus* is equal in volume to about four *Centropages*, and a 10 mm euphausiid is equal in volume to about four *Calanus*.

A number of the larval fish examined had empty stomachs (Tables 3–7). LEBOUR (1921) has suggested that, in herring, infrequent feeding coupled with rapid digestion would account for this. SHELBOURNE (1953) demonstrated the existence of a marked diurnal pattern of feeding activity for post-larval plaice. His conclusion that plaice larvae are visual feeders holds true for other fish as most of the eighteen species taken by LEBOUR (1919) and kept alive in aquaria were observed to be feeding by sight. Larval haddock kept in an aquarium at Woods Hole have been observed to be stalking their food visually. The fact, however, that many of the haddock, cod, and coalfish taken during daylight hauls had empty stomachs indicates that feeding is sporadic and digestion rapid. One haddock larva (5 mm) observed in our laboratory ate and digested three brine shrimp (*Artemia salina*) larvae in an eight-hour period.

Many of the larval fish larger than 9 mm were parasitized by a copepod ectoparasite, *Caligus* sp. (Tables 3–7). This parasite ranged in length from 1 to 4 mm and was encountered in all areas sampled. There were as many as four parasites on some larvae, attached mostly to the first dorsal fin and the opercle. It seems unlikely that this parasitism hampers the swimming ability and hence the feeding of the larvae since the stomachs of the parasitized fish contained as much food as unparasitized fish in the same area.

Although the structure and behaviour of the prey may play an important part in determining its vulnerability, the size of the zooplankters appear to be the most important factor in their utilization as food. This is related to the size of the mouth and gullet of larval fish. The larvae are "selective" in their feeding only in that they prey upon appropriate size groups. No selection of species was observed. The data presented indicate that the fish were feeding on the most abundant species of plankton present at the time but were restricted in their choice to animals of a certain size.

Summary

1. The stomachs of 536 larval haddock, cod, and coalfish were examined. These fish were taken in a 1 metre ring-net towed horizontally through surface waters in the Gulf of Maine, on Georges Bank, and at Woods Hole during the springs of 1953, 1955, 1956, and 1957.

2. In general, larval fish were eating the most abundant species of food but were restricted to animals of a certain size.

3. Of the many kinds of food available, adults and juveniles of four species of copepods and larval copepods contributed the major portion of the diet. The composition of the food was essentially similar for all years.

4. Fish larvae ranging in size from 4 to 18 mm fed mainly on larval copepods; whereas the bulk of the food of fish larger than 18 mm was adult copepods.

5. Parasitism by *Caligus* sp. apparently did not supress feeding.

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ANDELSBOGTRYKKERIET I ODENSE

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Comments on the Abundance and Ecology of the Ascidian *Amaroucium constellatum* in Sinepuxent and Chincoteague Bays[1]

ABSTRACT

The ascidian *Amaroucium constellatum* inhabits the shallow coastal Sinepuxent and Chincoteague Bays and was found predominantly over mud, mud-oyster, oyster bottoms or on pilings and occasionally on the oyster drill, *Urosalpinx cinerea*, where moderate currents and salinities above 28 ppt prevail. *A. constellatum* was also noted on sand bottoms to a depth of five fathoms in coastal waters near Chincoteague, Virginia.

Van Name (1945:38–40) and Miner (1950:848) stated that the ascidian *Amaroucium constellatum* Verrill occurs from Cape Cod to the Gulf Coast of Florida in one to 15 fathoms of water where it is most common on rocks (Costello, et al. 1957:202) and wharf pilings. Cowles (1930:366–7) in his study of Chesapeake Bay and its offshore waters did not record this species in the Maryland-Virginia area. Scott (1934:1–53; 1945:126–38; 1946: 66–80; 1952:226–47) has contributed greatly to the knowledge of the embryology and early development of this species. Data on the abundance, habitat requirements and occurrence of *A. constellatum* in seashore bays are lacking in the literature.

While conducting a monthly trawl survey in 1959, *A. constellatum* was found throughout Sinepuxent and Chincoteague Bays in Maryland and Virginia (Fig. 1), except for the Public Landing and Fox Hill Levels sample areas. Its absence in those areas could possibly be the result of the weak water currents or low salinities that persist there. Colonies 60 mm in diameter and 30 to 40 mm high were collected. Their texture and color agreed with that given by Van Name (1945:39), "Surface of colony is smooth and its texture gelatinous and only moderately firm. Test is opaque but the color of zooids renders them conspicuous. In life, color of test varies from cream color through various shades of yellow (or more frequently flesh-colored) to a pale orange or reddish." The cloacal chambers, however, did not contain the usual three to four bright purple tadpole shaped larvae (Verrill and Smith 1873:704). Numerous buds of developing zooids were found around the old colonies similar to that described by Berrill (1935:327–9). *A. constellatum* was found from April to December with the greatest number of colonies being collected between September and December. Greatest concentrations of this species occurred in December (Table 1) south of White Rock and in the area of Franklin City to Chincoteague, Virginia where the salinities were usually 28 ppt or more or near that of the adjacent ocean. In order to compare abundance between stations (each sample area was three-fourths of a mile long and 25 feet wide) a scale from 1–10 was devised. This scale was based on that portion of an ordinary 12 quart bucket that the sample occupied.

Wells (1957:124–6) characterizes the bottom of Sinepuxent Bay as mostly sand and mud. The western side of Chincoteague Bay, in general, has a mud or mud-oyster bottom while sand bottoms predominate on the eastern side of that bay. The latter are constantly shifted by the wave action that prevails in these readily wind-overturned shallow (average depth is six feet) bays. Perhaps it is this action that accounts for the absence or inability of this ascidian to remain attached to the sandy bottoms of the eastern portion of these bays. Evidence that partially bears out this premise stems from observations in the summer of 1957 when a small barrier fence was laid on the bottom near Mills Island. The fence was part of the copper barrier oyster drill control experiments of the U. S. Bureau of Commercial Fisheries. Great quantities

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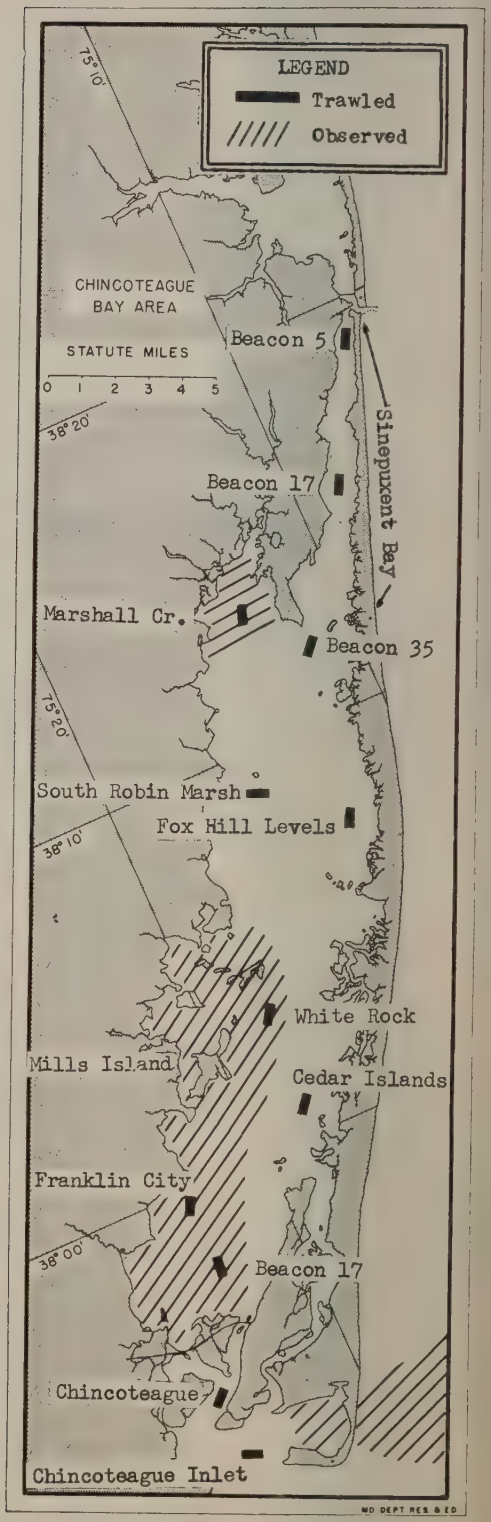

Fig. 1.—Areas inhabited by the ascidian *Amaroucium constellatum* in Sinepuxent and Chincoteague Bays.

TABLE 1.—Monthly abundance of the ascidian *A. maroucium constellatum* at sample sites throughout Sinepuxent and Chincoteauge Bays, 1959.

Locality	Month							
	April	May	June	July	August	Sept.	Oct.	Dec.
Beacon 5 Maryland	1	1	1	1	1	1	1	1
17 Maryland	1	1	1	2	2	1	1	2
35 Maryland	1	1	—	1	3	2	1	2
Marshall Cr.	—	—	—	—	2	2	1	1
South Robin Marsh	—	—	—	—	—	—	—	—
Fox Hill Levels	—	—	—	—	—	—	—	—
White Rock	1	1	1	1	3	4	3	3
Cedar Islands	1	1	1	5	3	2	1	1
Franklin City	3	3	4	5	6	7	9	10
Beacon 17 Virginia	3	3	5	5	5	6	8	10
Chincoteague City	—	—	—	1	1	1	1	1
Chincoteague Inlet	—	—	—	—	—	—	—	1

of these ascidians, 30–60 mm in diameter, had drifted against this fence each week, apparently after having broken away from previous attachments. Thus, in Sinepuxent and Chincoteague Bays *A. constellatum* is found on mud, mud-oyster or oyster bottoms, contrary to that noted for most species of *Amaroucium* (Van Name 1945:1–38). However, when found on a mud bottom *constellatum* is almost always found attached to oysters, shells, or some other hard object. Occasional small colonies are often found attached to the oyster drill, *Urosalpinx cinerea* (Say). Likewise *A. constellatum* was commonly found attached to oyster stakes (poles used to mark the boundaries of leased oyster grounds) south of White Rock. *A. constellatum* is also known in the coastal waters off Chincoteague, Virginia (Fig. 1) over sand bottoms to a depth of five fathoms.

Although *A. constellatum* has been found elsewhere, together with the similar ranging *A. pellucidium* (Van Name 1945:40), which Grave (1921: 1–4; 1922:27–33) has shown to be distinct, the latter species was not discovered. *A. pellucidium* is a deeply cleft, sand encrusted-embedded form whose stomach is bright red. Likewise *pellucidium* seems to prefer sandy bottoms and swift tidal currents (Grave 1921:38). Perhaps it will be found in the inlets near Ocean City, Maryland or Chincoteague, Virginia, which areas would fulfill the ecological requirements of this species. Of the 22 recognized species of *Amaroucium* (Van Name 1945:21) the only other synoicid ascidian that could possibly be present in these waters is the smooth, whitish, platelike (one to two inches long, six inches high and one inch thick) *A. stellatum*. If *stellatum* is present in these waters it might also be found with *A. pellucidium* over sandy bottoms with extremely swift currents.

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